COMPARATIVE FEEDING BEHAVIOUR AND MORPHOLOGY OF MYSIDS (CRUSTACEA: MYSIDACEA)

by

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STATEMENT

I hereby declare that this thesis contains no material which has been accepted for the award of any other degree or diploma in any other tertiary institution.

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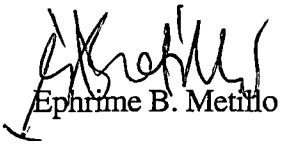

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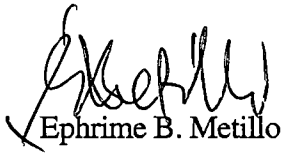

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ABSTRACT

Behavioural and morphological studies were made to determine whether feeding niche partitioning occurs in three sympatric coastal mysids, *Anisomysis mixta australis*, *Paramesopodopsis rufa*, and *Tenagomysis tasmaniae*.

All three species showed optimal chemoreception as judged from stereotyped food capturing response to mixtures of feeding stimulant (either betaine-HCl or glycine) and suppressant (ammonia). The strongest responses were to 50:50 mixtures of both betaine-ammonia and glycine-ammonia solutions. In general, the response curve to the different mixtures tested was bell-shaped. *A. mixta australis* only showed the normal curve in response to the glycine-ammonia mixture. The platykurtic curve in *T. tasmaniae* suggests less optimal response to the betaine-HCl-ammonia solution. *P. rufa* reacted more strongly to the betaine-ammonia than to the glycine-ammonia solutions, and more of its individuals responded to both solutions than the other two species. These results suggest that sensitivity to betaine-HCl- and glycine-rich fresh and decomposing animal tissue is most sharp in *P. rufa*. Acuteness, however, may be diminished with duration of decomposition as indicated by reduced responses to mixtures with >50% ammonia. High concentrations of either stimulant also had a suppression effect.

Similar mechanisms are used by all three to capture fine particles. Particle size selection overlapped in the two larger species, *P. rufa* and *T. tasmaniae*, which ingested a full range of sizes of inert beads from 10 to 90 μm. The smallest species, *A. mixta australis*, differed from the other two by mainly ingesting the smallest beads.

P. rufa and *A. mixta australis* both form their feeding appendages into 'cages' (primary composed of mouthparts and the secondary of thoracic endopods) to grasp live prey. *T. tasmaniae* uses mainly the primary cage because its thoracic endopods remained spread, a feature associated with its behaviour of resting on the substrate. *P. rufa* was the most efficient predator of the euryhaline daphniid prey, *Daphniopsis australis*. It showed a steeper linear functional response curve for this prey than the two other species which showed similar flat linear curves. All three species showed

similar predation success on *Artemia* sp. nauplii, and similar predation failure for the calanoid copepod *Gladioferens pectinatus*.

In situ feeding selectivity experiments using ^{14}C-labelled *Artemia* sp. nauplii and phytoplankton, and ^{3}H thymidine-labelled macroalgal detritus showed that all three species preferentially ingested the animal food, *i.e. Artemia* sp. nauplii.

The activity of the digestive enzyme laminarinase was analyzed over one year to assess herbivorousness in the three mysid species. High levels of activity in *T. tasmaniae* were sustained throughout the entire year and peaked in August. *P. rufa* showed levels 2.5 to 4 times lower than those in *T. tasmaniae*, and remained constant through the year. *A. mixta australis* showed a bimodal pattern with peaks in February and August comparable to those in *T. tasmaniae*. The minimum levels were similar to those in *P. rufa*. Significant interaction between species and sampling date suggests that the peak of activity in August (late winter) may be associated with all three species ingesting relatively high levels of macroalgal detritus. The peak in February (late summer) shown by *A. mixta australis* reflects similar high levels of consumption of both macroalgal and laminarin producing phytoplanktonic particles. Short term (24 h) starvation reduced activity in *P. rufa*, but not in the other two species. Medium term (9 d) feeding on the non-laminarin producing dinoflagellate, *Scrippsiella trochoidea*, reduced activity in *T. tasmaniae* on day 9, and on day 5 in *A. mixta australis*. However, the latter species returned to the initial levels on day 7. No definite conclusion can be drawn from the *P. rufa* results, because all animals died after 3 d. Marked reduction in activity was also observed when juveniles of *T. tasmaniae* and *A. mixta australis* had grown to maturity using *Artemia* sp. nauplii as food. Therefore, laminarinase is likely to be substrate specific in *T. tasmaniae*, but not in *A. mixta australis*.

Growth rates of the juvenile stages of the three species held separately in the laboratory were similar when fed with excess amounts of *Artemia* sp. nauplii. When all three species were held together and fed with reduced amounts of nauplii, *P. rufa* grew faster than the other two species which showed similar rates. Of the three species, only a few *T. tasmaniae* individuals showed slight growth when fed aged

algal detritus and the diatom *Phaeodactylum* sp. Although *P. rufa* grew best on animal food the other two species are equally dependent on the same type of food.

Foregut and mouthparts morphological data indicate three major feeding adaptations: predominantly macrophagous feeding on tough macrophyte particles (type Ia) for *T. tasmaniae*, predominantly macrophagous feeding on large animal prey/detritus (type Ib) for *P. rufa*, and mainly microphagous and/or suction feeding on smaller animal prey and fine particulate matter (type Ic) for *A. mixta australis*.

These studies suggest that probable strong competition associated with overlapping feeding habits in the three species is reduced by differences in size and feeding structure, and by microhabitat partitioning (shown by other authors) with *P. rufa* and *A. mixta australis* spending more time aggregated in the water column while *T. tasmaniae* is found on, or a few centimetres above, the sandy substrate.

The foreguts of 45 more species, three from Tasmania and 42 from different biogeographical zones of the globe, were surveyed to test the hypothesis that feeding adaptation is more important than phylogeny in shaping foregut structure. The spheroidal shape shown in the initial three Tasmanian species, and the tubular form were the two main foregut types observed. From evidence on diet and feeding behaviour, a series of four basic feeding adaptations were recognized: the three types (Ia, Ib, Ic) found in the initial three Tasmanian species, and the mainly suction feeding exemplified by the tubular foregut type (type II). Cladistic analysis suggests that the type I adaptations appear to have evolved several times within clade. The specialized suction feeding seems to have been derived from type Ia. These data suggest that the need to collect food seems to have been such a strong selective force that adaptations of the feeding apparatus have masked phylogenetic relationships within these structures in mysids.

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CONTENTS

CHAPTER 1

GENERAL INTRODUCTION

The beauty of nature lies in detail; its message in generality.

S. J. Gould, *Wonderful Life*

Functioning of ecosystems is shown in the manner their structured components transduce light energy from the sun to another form of energy (Lindeman 1942; Krebs 1985). In the aquatic ecosystem, it is generally recognized that energy flow may be more dependent on body size and feeding patterns than on the taxonomic structure (Steele and Frost 1977). The feeding niches of species in the aquatic environment are diverse partly because the food resource is diverse. Biological interactions among these aquatic species may further increase the diversity of feeding patterns.

Characterized by a high diversity of productive habitats, *e.g.* mudflats, kelp forests, seagrass meadows, coral reefs, mangals or mangrove systems, saltmarshes, and a planktonic system, the coastal region, the region of transition between the land and the open seas, represents one of the most dynamic ecosystems in the biosphere (Mann 1982; Parsons *et al.* 1984b; Barnes and Hughes 1988). According to Kjerfve (1986), the coastal region may be divided into three parts: (a) the riverine zone, (b) the estuarine mixing zone, and (c) the nearshore zone. Almost always present in these zones are the cosmopolitan mysids (Mauchline 1980). The main concern of the present thesis is to demonstrate the usefulness of the competition, niche, and resource partitioning theories in explaining the trophic role of co-occurring nearshore mysids.

Background Information on Mysids

Distribution, Size, and Behaviour

Mysids are shrimp-like crustaceans most species of which aggregate in large numbers in marine, estuarine, and freshwater habitats (Tattersall and Tattersall 1951; Mauchline 1980). Females in breeding condition possess the characteristic brood

pouch which gave the group its common name, opossum shrimps. Studies done on the biology, ecology, geographical distribution, vertical migration, biochemistry, and the role of mysids in the marine economy are reviewed by Mauchline (1980). Morgan (1982) also provides an account primarily of the ecology of freshwater mysids in the Great Lakes.

The Order Mysidacea consists of two Sub-Orders, Lophogastrida distinguished by the presence of gills on the thoracic appendages and Mysida which includes the majority of species (Tattersall and Tattersall 1951). Usually present in the Sub-Order Mysida is a pair of statocysts on the tail appendages (endopod of uropods). Lophogastrid mysids range in length from 17 to 350 mm (except the genus *Paralophogaster*), while members of the Sub-Order Mysida, have average adult body lengths less than 15 mm (Mauchline 1980). Nearshore mysids are classified as micronektonic and are capable of maintaining position against water movements (Clutter 1969; Mauchline 1980; O'Brien and Ritz 1988; Hough and Naylor 1992). They are known to avoid strong currents and form swarms in protected areas of the coasts (Mauchline 1980). Gregariousness and various forms of aggregation in mysids have been studied (Wittmann 1977; Mauchline 1980; O'Brien 1987).

Predators and Feeding

Mysids form an important food item for fish, marine birds, invertebrates, and to a limited extent are even eaten by man (Omori 1978; Mauchline 1980).

Greene's (1985) classification scheme for dividing planktivorous predators into functional groups categorized mysids as invertebrate raptorial predators which use both cruising and ambush encounter tactics. His classification is certainly not true of all mysids since some species can suspension feed upon phytoplankton and detritus particles (Cannon and Manton 1927; Clutter 1967; Bowers and Grossnickle 1978; Mauchline 1980; Grossnickle 1982). Regarded as universally omnivorous, mysids exhibit a range of feeding modes from filter-feeding on phytoplankton to carnivory, with detritus being a major component of the diet of many species (*see* review by Mauchline 1980). Nevertheless, predatory species may exert strong size-selective

feeding and structuring of zooplankton (*e.g.* Kost and Knight 1975; Fulton 1982; Bowers and Vanderploeg 1982; Nero and Sprules 1986) and meiobenthic populations (Johnston and Lazenby 1982). Mysids are also capable of size selective herbivorous (Bowers and Grossnickle 1978; Grossnickle 1979) and detritivorous (Mullin and Roman 1986) feeding.

The Concept of Ecological Niche

Central to the theme of the present thesis is the concept of niche. Joseph Grinnel in 1924 coined the word "niche" to refer to an animal's ultimate distributional unit in the biosphere (see DeBach 1966; Vandermeer 1972; Krebs 1985; Schoener 1989; Pianka 1994). Elton (1927) defined a niche as the functional role and position of an organism within a community, emphasizing trophic relationships with other species. The latter definition has been recognized as the best description of a niche while Grinnel's definition best describes a habitat (Whittaker *et al.* 1973). Hutchinson (1957, cited in Schoener 1989) introduced aspects of the ecological niche emphasizing the organism and its interaction with its biotic and abiotic environment. In the absence of competitors the entire set of resources a species can exploit comprises its fundamental niche (Hutchinson 1958, cited in Krebs 1985). According to Hutchinson, since a certain resource represents a niche axis, the fundamental niche of an organism comprising many axes, may appear as an *n*–hypervolume plotted in a multidimensional space. With the presence of competitors, the fundamental niche of a species is not fully exploited, hence in a given time and space the species can only utilize a narrow range of resources or its realized niche, which is actually a subset of the fundamental niche (Levinton 1982; Pianka 1994). The fundamental niche must remain an abstraction because of the impossibility of knowing all possible factors impinging upon an organismic unit (Pianka 1994).

The modern theory of the ecological niche has been more linked to resource utilization, and directed towards systems in which resource competition predominates (Schoener 1989; Pianka 1994). Overlap of resource utilization is a common outcome in

two interacting species with similar requirements. If the demand for such a resource is higher than its availability, the resource becomes limiting, and strong competition becomes inevitable, leading ultimately to species exclusion. In simple systems, degree of overlap of resources or the strength of competition may be expressed using the coefficient α derived from the Lotka-Volterra equation (Levinton 1982; Krebs 1985; Schoener 1989). In nature, despite the apparent likelihood of food resource becoming limiting it has been commonly observed that exclusion of species brought about by a strong overlap of niches is rare because species have evolved means of niche partitioning (Krebs 1985). Niche dimensions which are often partitioned in order to avoid competition are microhabitats exploited, foods eaten, and times of activity (Schoener 1974; Pianka 1994).

From the recent synthesis of Schoener (1989), has come the recognition that apart from the niche theory, several other ecological theories (pluralism) are needed to explain patterns and processes in competitive communities. Schoener noted that because the detailed assumptions of a model includes inherent biological variability, the mechanistic (reductionist) approach has become important. The approach is a theoretical programme in which community- and population-level theory is derived mainly from theory at individual levels, *i.e.* behavioural ecology, physiological ecology, and ecomorphology. The same approach has given impetus to the present thesis, and the three biological disciplines mentioned have guided the various observational and experimental aspects of the present study.

Competition, Coexistence, and Resource Partitioning

Considered one of the fundamental concepts of ecology and assumed to be one of the driving forces of evolution by natural selection, competition is defined by Milne (1961 cited in Law and Watkinson 1989) as the endeavour of two (or more) animals to gain the same particular resource when that supply is not sufficient for both (or all). Its forms include (a) interference or contest: when individuals engage in direct conflict or aggression for a limited resource (*e.g.* food and mate), and (b) exploitation or

scramble: when organisms are unaware that they are consuming similar limited resource (Law and Watkinson 1989). Classic studies on desert ants and rodents, lizards, bumblebees, barnacles, hermit crabs and tits have generated three syntheses concerning the role of inter-specific competition (see review by Begon and Mortimer 1986):

1) competition is occurring at present. By careful experimental manipulations in the field usually done by excluding one of the competing species, realized niche dimensions of the other competing species may be changed or modified so that it achieves its fundamental niche.

2) competition may have occurred in the past over an evolutionary time scale. If inter-specific competition reduces fitness, in two or more competing species in the past, then these species must evolve means of diminishing competition for a limited resource which further results in slight (apparent) or distinctive (explicit) differences in phenotypic characters as in character displacement (Brown and Wilson 1956; De Bach 1966; Fenchel 1975; Schoener 1974, 1982; Vandermeer 1972; Arthur 1982; Branch 1984; Pianka 1994). On the other hand, each of these species must also adjust to the fact that similarities within the same population encourage severe intra-specific competition, therefore they must also evolve means of offsetting this pressure. As a result, a compromise between pressure from conspecific and inter-specific competition is constantly being sought by different species. Size of the species and specialized feeding structures are commonly used to demonstrate evolutionary pressure from past inter-specific. More often differences in size (Hutchinson (1959), but see Simberloff and Boecklen (1981)), the sizes of the different food they consume, and foraging strategies (*e.g.* Vanderploeg 1990; Rothhaupt 1990) are frequently cited as means of resource partitioning between co-existing species.

3) the possibility that competition does not occur at all. This may be deduced if spatio-temporal resource partitioning mechanisms (differences in morphological features, feeding strategies, habitat preference, environmental tolerance, site location etc.) are strongly demonstrated, and fitness (survivorship, fecundity, or reproductive output) from experimental manipulations (perturbation of current ecological status

preferentially field or as close to natural conditions as possible) is not affected or stays at a similar level with or without the presence of a competitor. Hence, if the latter conditions are not met, interpretations from morphological differences and other resource partitioning mechanisms do not necessarily mean competition occurs among co-existing species.

Differential seasonal utilization of resources by competitors is also an alternative mechanism of competitive coexistence (Levins 1979). Diffuse competition among components of a community may be commonplace and may be the prominent mechanism involved in resource partitioning (Begon and Mortimer 1986). In diffuse competition, the total competitive effects of many species are much reduced (MacArthur 1972; Pianka 1994).

Resource partitioning, on the other hand, is not the ultimate means of mediating coexistence. Species may coexist merely because the environment is rarely stable for long enough periods for competition to become important (*e.g.* Andrewartha and Birch 1954, cited in Schoener 1982; Simberloff 1976; Wiens 1977; Connell 1978, 1980). Wiens (1977) believes that species relationships and community organizations are produced by species-specific pre-adaptations to different resources and varying mixtures of processes such as competition, predation, physical disturbance, or recurrent but unpredictable environmental fluctuations. As a counter-argument, Schoener (1982) dismissed Wiens' propositions on the grounds that from many field experiments in environments which are highly variable (*e.g.* deserts), competition is still apparent and assumptions of the competition theory still hold. Competition and the different ecological theories it has spawned, therefore, need to be viewed not as an "all-or-none" phenomenon because in nature different organisms may experience a continuum of ecological circumstances for which it may or may not be necessary to invoke competition as the only forcing function (Pianka 1994). More data from different life forms are still needed to acknowledge or discredit the importance of the competition, and niche partitioning theories (Branch 1984; Hines 1985).

Coexistence of species in a rocky intertidal community has been shown to be an outcome of the structuring effect of predation (Paine 1966). The predation theory was

developed from the observation that keystone species maintain diversity of co-existing species at the base of the food chain by selectively preying upon species which are superior competitors. Physical disturbance (*sensu* Connell 1961) and the number of trophic levels (trophic complexity), both of which correlate with temporal and spatial heterogeneity, may interact in a multivariate manner controlling predation effects and the structure of communities as a whole (Menge and Sutherland 1976). Predation has also been suggested as an organizing force in oceanic zooplankton communities (McGowan and Walker 1979, 1985).

In contrast, Longhurst (1985) emphasized that oceanic zooplankton diversity (and coexistence) may be explained by the vertical structuring of the pelagic realm, and that contemporaneous disequilibrium (*sensu* Richerson *et al.* 1970) within the depth zones of these vertical layers may be important in maintaining local diversity. The contemporaneous disequilibrium hypothesis, which sprung from Hutchinson's (1961) "paradox of the plankton", states that the amount and scale of turbulence in the pelagic environment forms parcels of water each having characteristics matching the requirements of one or more species, and these features should exist for periods longer than the turn-over time of each species (Longhurst 1985). In this way, different species could be at competitive advantage in each patch preventing competitive exclusion, and a stable equilibrium favouring only one or a few species is never reached (Longhurst 1985).

Competition and Resource Partitioning in Mysids

A high coincidence of spatial co-occurrence has been shown by the mysid community sampled from the North American Atlantic Coast (Wigley and Burns 1971). For example, of the 19 species collected, the species pair with similar body length *Bowmaniella portoricensis* and *Anchialina typica*, occurred within an area of 0.48 m^2, while *Neomysis americana* and *Mysidopsis bigelowi* occurred within an area of 0.1 m^2. Wigley and Burns (1971) noted that the coexistence of these mainly shore species does not suggest that they are straightforward competitors, instead such co-occurrence

serves as a strong indicator of possible competition for space or other living requirements. An extensive sampling across the Cape Cod Bay in the same region has revealed seven mysid species, four of which have shown pairing after correlation with substrate type and bathymetry (Maurer and Wigley 1982). *Neomysis americana* and *Mysis stenolepis* formed the inshore species pair which occurred in the 10-29 m depth range and in substrates with clayey-silt. The other offshore species pair, *Erythrops erythrophthalma* and *Mysis mixta* occur in deeper regions (20-39 m) and in finer substrates with clayey-silt and silt. The zonation pattern of these mysid species has been noted to be indicative of reducing competition for space. Finfish predation has also been suggested as a structuring force of the spatial distribution of these mysid species.

Wooldridge and Bailey (1982) reported that the three mysid species in the Sundays River Estuary in South Africa show distinct zones of maximum distribution. Although two of these species, *Rhopalophthalmus terranatalis* and *Mesopodopsis slabberi* (see footnote)[1] showed overlapping horizontal spatial distribution, a vertical separation was also evident in that the former species dominated in the bottom water while the latter was often collected near the surface. Having a similar diet of detritus and phytoplankton, the third species, *Gastrosaccus brevifissura* occurred mainly at the mouth of the estuary. *Rhopalophthalmus terranatalis*, the predominantly carnivorous mysid showed a strong preference for juvenile *Mesopodopsis slabberi* (Wooldridge and Webb 1988). The predatory species is often sympatric with *M. slabberi* which is mainly a detritus and phytoplankton feeder. Predation rates of *R. terranatalis* have indicated a strong potential for reducing recruitment into the population of its prey. Coexistence of the two species is facilitated by the diffuse distribution of the predatory species (Wooldridge and Webb 1988).

The parallel to the shore zonation of nine hypopelagic and benthic mysid species in the La Jolla bight of California can be explained by the food distribution which is imposed by the water circulation system along the coast (Clutter 1967). The nearshore circulation system in this area continually re-suspends food particles and sediments. Although exerting a weak explanatory power, other factors such as bottom topography,

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[1]The taxonomy of *M. slabberi* has recently been revised by Wittmann (1992).

water temperature-associated internal waves, threshold light intensity, character of substrate (a physical property affecting distribution of mysids, which was studied in detail by Wittmann 1977), and distribution of predators may influence the mysid spatial distribution. Clutter (1967) suggested that zonation of these mobile marine invertebrates is a manifestation of apparent competition for space rather than direct competition for food.

Many Tasmanian shallow inshore areas are inhabited by a number of mysid species, and three of the most abundant ones, *Paramesopodopsis rufa*, *Tenagomysis tasmaniae*, and *Anisomysis mixta australis*, have been found to occur in similar habitats (Fenton 1986, 1992). They occupy a similar depth range of 1.2 to 6 m, and a certain degree of microhabitat partitioning has been observed in the field (Fenton 1992). In the daytime, *P. rufa* and *A. mixta australis* spend more time aggregated in the water column while *T. tasmaniae* is found on or a few centimetres above the sandy substrate. The major peaks of abundances of these three species are temporally separate (Fenton 1992, 1994).

Gut content analysis reveals that these species have an overlapping diet of macroalgae, crustacean remains, pine spores, dinoflagellates, and a large proportion of amorphous detrital materials (Fenton 1986). This overlap of diets suggests a potential for competition for similar food resources in the three mysid species. However, there are indications of dietary preference in each. Crustacean fragments formed a large portion of the diet of *P. rufa*; macroalgal fragments are most common in the guts of *T. tasmaniae*; and fine detrital matter mainly comprised the stomach contents of *A. mixta australis*. Stable carbon and hydrogen isotopes analysis have shown that diets of *A. mixta australis* and *T. tasmaniae* are essentially the same (Fenton 1986).

Aims of the Study

The objectives of the present study were two-fold: the first was to investigate at a much finer scale the feeding niche separation suggested earlier (Fenton 1986) in the three most common and co-occurring mysid species. A detailed examination of the

feeding behaviour and morphology of these three species was undertaken. The behavioural aspects are investigated by (a) optimal chemoreception, (b) micro-videographic filming of suspension and predatory feeding mechanisms, (c) feeding selectivity experiments, both *in situ* and in the laboratory, (d) indirect assessment of herbivorousness using a digestive enzyme (laminarinase) assay, and (e) survivorship and growth on different diets. The morphological aspects are examined by ultrastructural observation of cephalothoracic feeding appendages and the foregut. The second objective was to attempt to relate feeding adaptations and phylogeny in co-occurring mysids.

CHAPTER 2

OPTIMAL CHEMORECEPTION STUDY

Introduction

The aquatic environment may be perceived as a cocktail of chemical stimuli for organisms which rely on the chemosensory modality (Carr 1988; Kamil 1988; Zimmer-Faust 1989). Chemosensory feeding and its underlying complex and dynamic mechanisms have been reported in many groups of invertebrates (see reviews by Lenhoff and Lindstedt 1974; Mackie and Grant 1974; Ache 1982; Atema 1985; Carr 1988). Crustaceans, for example, display stereotyped and non-stereotyped feeding behavioural responses after chemostimulation using extracts or low molecular weight compounds (amino acids, quaternary ammonium compounds [trimethylamine oxide or TMO, betaine, homarine], nucleotides, nucleosides and lactate) similar to those found in prey organisms or potential food sources (*e.g.* Crisp 1967; Fuzessery and Childress 1975; Hamner and Hamner 1977; Hamner *et al.* 1983; Robertson *et al.* 1981; Poulet and Ouellet 1982; Carr and Derby 1986; Carr 1988; Derby and Atema 1988; Zimmer-Faust 1989; Strand and Hamner 1990).

Our knowledge of chemosensory feeding has been based largely on the adaptive hypothesis in which it is implicitly assumed that the response magnitude varies directly with the relative concentration of substances in prey, thus allowing animals to locate potential food items more efficiently (Weissburg and Zimmer-Faust 1991). The chemical properties of potential food may function as olfactory and/or gustatory cues. These play a significant role in crustacean food/prey selection (Atema 1985; Carr 1988; Zimmer-Faust 1989). In the actual capture and subsequent ingestion of suspended food particles chemosensory control has been emphasized in crustaceans (*e.g.* Poulet and Marsot 1978, 1980; Hamner and Hamner 1977; Hamner *et al.* 1983; DeMott 1989). For instance, contact chemoreception is the mechanism thought

responsible for stimulation of the food capturing response in crustaceans and subsequent ingestion (Crisp 1967; Carr 1978; Fuzessery and Childress 1975).

The optimal chemoreception theory proposed recently by Zimmer-Faust (1987) highlights the strong response by crustaceans to odours that specify food of highest energy and nutrient content. A mixture of stimulant and suppressant compounds (amino acids and ammonia, respectively) present in the food would trigger varying reactions, and the organisms' responses thus depend upon their relative optimum chemosensory feeding adaptations. For example, organisms feeding mainly on detritus showed a feeding response to ammonia which is an inhibitor to other organisms which feed least on detritus. Zimmer-Faust (1993) has recently shown that phago-stimulation in spiny lobster follows a decreasing trend as food freshness decreases which is reflected in the concentration of ATP, ADP, and AMP. The role of suppressants makes the use of single compounds in assays questionable because it may not properly define the natural range of sensitivities of test animals (Zimmer-Faust *et al.* 1984; Zimmer-Faust 1987, 1989).

Environmental constraints and behavioural requirements or adaptation to the environment would lead to substantial differences in sensitivity to food stimuli between species (Derby and Atema 1988). In a comparative study between littoral and deep sea dwelling crustaceans, Fuzessery and Childress (1975) have noted differential sensitivity to dissolved compounds between these groups of animals. Although both groups of animals responded to a host of chemostimulants, the deep sea crustacean, represented by the lophogastrid mysid, *Gnathophausia ingens*, showed a relatively higher chemosensitivity level than inshore decapod crustaceans. This may be attributed to the fact that the deep sea crustaceans could not afford to sloppy feed in a low food level environment. Therefore, upon capture of food particles, extremely low concentrations of chemostimulants would be enough to instigate subsequent food ingestion and processing. Interspecific differences in sensitivity may be related to feeding habits and types of food in their diets (Derby and Atema 1988). For instance, the marine herbivorous crab *Pugettia producta* shows a greater response to some sugars than to many amino acids (Zimmer *et al.* 1979). Similar results have been

reported in the sand fiddler crab *Uca* (Robertson *et al.* 1981; Weissburg and Zimmer-Faust 1991). Co-occurring copepods *Acartia hudsonica* and *Eurytemora herdmani* both showed chemosensory feeding response to amino acids, but *A. hudsonica* was stimulated mostly by aliphatic amino acids (*e.g.* leucine and valine), whereas *E. herdmani* was most responsive to dicarboxylic amino acids (*e.g.* glutamic acid and aspartic acid) (Poulet and Ouellet 1982).

Although vision and mechanoreception are important in mysid feeding, Ramcharan and Sprules (1986) and Crouau (1989) acknowledge the importance of chemoreception. In the present study, optimal gustatory chemoreception to different mixtures of the tertiary amine, betaine-HCl, or the amino acid, glycine (feeding stimulants), and ammonia (feeding suppressant) is examined in three co-occurring mysid species.

Materials and Methods

Experimental Animals

Mysids were collected off Taroona Beach, 10 km south of Hobart, south east Tasmania. The detailed description of the sampling area is in chapter 6 where *in situ* feeding studies were explored. Swarms of the three species were located by skin and SCUBA diving, and collected using a hand-held dip net with 1 mm mesh size. Care was taken to ensure that the mysids in the net remained underwater until their quick transfer to 20-L buckets of seawater. Collected animals were transported to the laboratory, carefully transferred into a 50-L tank containing 5 µm Millipore-filtered seawater, gently aerated, kept at ambient temperature (12-14 °C), and fed with powdered fish meal pellets. An appreciable number of the three species survived for three weeks under these conditions, but animals used in the present study were kept in the laboratory for not more than two weeks prior to experimentation.

Mysid Tethering and Filming Set-up

Observations were conducted on fed mysid individuals which were individually tethered to thin (ϕ = 0.5 mm) stainless steel rods. Tethering was done by attaching one end of the rod to the mid-dorsal surface of the mysid carapace using 'Super Glue', a quick drying and non-toxic adhesive. Tethered individuals remained healthy, actively moving their exopods for a maximum of 6 days. However, in order to minimize stress, videotaping of the chemosensory feeding behavior was carried out 2 days after the animals were tethered.

The filming set-up comprised a video camera (Panasonic CCTV, Model WV-BL600/B) mounted on a Wild stereomicroscope (set at 60x magnification) alongside the tank (Fig. 2.1). The camera was connected to a high resolution black and white TV (National, Model WV-5410) and to an S-VHS video cassette recorder (Panasonic, Model NV-FS100HQ). An Intralux 5000 fibre optic source provided illumination. To start a filming session, a tethered mysid was quickly transferred to a glass tank (4.5 L; 25 x 10 x 18 cm), and submerged to a depth of 5 to 7 cm from the surface. The other end of the wire was anchored with Blu-tack to the edge of a 5-mm thick plexiglass plate (20 x 3 cm) along the top of the tank, and the desired position and plane of view of the animal obtained. A recirculating bath kept water temperature constant (13-14 °C) in the aquarium. Salinity was also kept constant (34-35 ‰) in all filming sessions.

Test Substances

From preliminary observations, 10^{-3} M of the tertiary amine betaine-HCl (Sigma-Aldrich Pty, Ltd., Australia) alone elicited stereotyped food capturing responses in the three mysid species. Dissolved betaine-HCl has been reported as a potent feeding incitant in fish (*e.g.* Mackie 1973; Mackie and Mitchell 1982), and in various crustaceans (Carr 1978; Carr 1988; Harpaz and Steiner 1990). Along with other tertiary amines, betaine may be perceived by chemoreception of a chemical

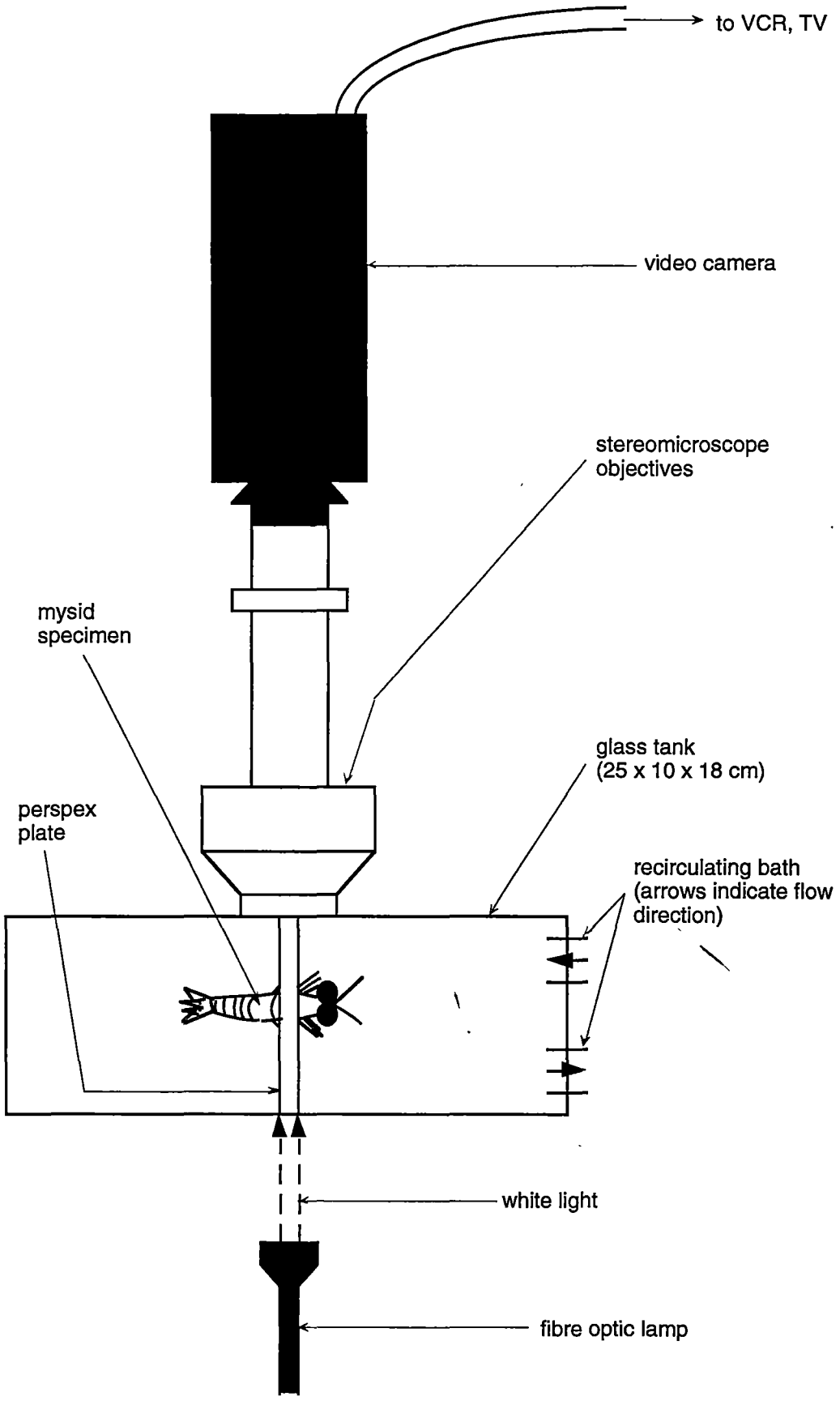


Figure 2.1 Top view of apparatus for recording mysid behaviour. (not to scale).

gradient from leakage of this compound from decomposing animal or zooplankton prey tissues (Crisp 1967; Fuzessery and Childress 1975). Betaine, a methylated amino acid form is found in the blood and excretory products of both vertebrates and invertebrates (Laverack 1963 cited in Laverack 1988). Betaine's $(CH_3)_3$-N moiety is most likely the active part of the molecule since it is common to the other tertiary amine compounds (Mackie and Grant 1974). As betaine-HCl, it may mimic the phago-stimulating property of amino acids because of its zwitterionic conformation (Fuzessery and Childress 1975). Carr *et al.* (1984) considered betaine as a potentiator of other amino acids in eliciting the grasping reactions of the shrimp *Palaemonetes pugio*. At levels comparable to those which the chemoreceptors encounter in nature, betaine and other compounds such as glutamate, glycine, taurine, arginine, introduced singly are capable of eliciting stereotyped feeding behavioural responses (Carr *et al.* 1984; Derby and Harpaz 1988; Derby and Atema 1988).

Also from a preliminary observation, 10^{-3}M glycine also stimulated capturing response in these animals, but it was not as potent as betaine-HCl. Zimmer-Faust (1987 and authors cited therein) noted that glycine at concentrations similar to that in prey tissues has been shown to maximally excite crustacean feeding. Glycine was most stimulatory to decapod and the deep-sea mysid crustacean, *Gnathophausia ingens* (Fussesery and Childress 1975). The choice of 10^{-3} M ammonia (AR grade, May and Baker Chem. Co., Australia) as the feeding suppressant was based on the findings of Zimmer-Faust (1987). These test stimuli concentrations are well above the background concentration of betaine-HCl and other amino acids in seawater which range from 10^{-8} to 10^{-9} M, but fall within the range of concentration found in tissues (Carr 1988 and references cited therein). All test substances were prepared using sterilized 0.8 µm (pore size) Millipore-filtered seawater. For the actual behavioural assay, the preparation of stimulant and suppressant solutions follows that of Zimmer-Faust (1987), *i.e.* five treatment solutions: 100% of either stimulant + 0% ammonia, 75% of either stimulant + 25% ammonia, 50% of either stimulant + 50% ammonia, 25% of either stimulant + 75% ammonia, and 0% of either stimulant + 100% ammonia, and a control which was the sterile seawater used in the preparation of the

chemical solutions. All pH-adjusted (pH = 7.2) mixtures were stored in chromic acid cleaned glass reagent bottles.

The Chemosensory Feeding Behavioural Assay

A total of 198 *Anisomysis mixta australis*, 246 *Paramesopodopsis rufa*, and 216 *Tenagomysis tasmaniae* adult individuals were used for the feeding behavioural assay. Fifteen to twenty six individuals for each test solution were used in the assay, which was performed 1-2 days after mysid tethering. Prior to filming, the tethered mysid was allowed to acclimatize in the filming tank for 3-5 minutes, then test substances were introduced. All experiments followed the double-blind assay (*sensu* Zimmer-Faust 1987) in which the experimenter does not know the different chemicals being introduced, and the person who keeps the codes for each test solution does not know the outcome of the experiments until revealed by the former. One mL of a test solution was introduced 1 cm in front of the tethered mysid using a Pasteur pipette. Average flow speed of the introduced test solution was 0.12 mL s^{-1}. Prior to introduction of each test solution, 1 mL of seawater from the tank was also introduced to observe chemo- and/or mechano-sensory behavioural response of the subject. The observations following this procedure were termed the response to seawater blank or control 2 as distinct from the control seawater test solution (control 1). Filming started 10 to 15 s before the introduction of test solutions, and stopped 10 to 15 s after introduction. The video-recording was viewed three times to confirm the type of response.

The ratios of the different test solution will follow the convention of stimulant (either betaine-HCl or glycine) first then ammonia, *e.g.* the mixture 50% betaine-HCl and 50% ammonia = 50:50.

Results

The following are the set of various limb postures sampled as feeding

behavioural responses to the test compounds:

1) food capturing response - sudden outsplaying of limbs, violent movements of mouthparts, scooping (fling and clap) posture of endopods, mandibular chewing, stomach activity, mandibular palps in primary cage formation (cf in chapters 3 and 4), and frequent antennular grooming. These series of acts have been considered as a response to contact chemoreception (Zimmer-Faust 1987 and references cited therein). In *T. tasmaniae*, the response involves the formation of the primary cage, rapid "fling and clap" movements of the endopods, and the second maxillipeds inside the cage scooped rapidly while the rest of the mouthparts vibrated rapidly. Unlike the other two species, food capturing in *T. tasmaniae* comprised this combination of feeding acts because in this species the endopods were spread prior to stimulus introduction.

2) tail flip - the abdomen and uropods curved ventrally perpendicular to the horizontal axis of the body.

The three species did not respond to the tank seawater (control 2). Food capturing and tail-flipping behavioural responses were compared only to the seawater control (control 1).

Response to Betaine:Ammonia Solution

Food Capturing Response

Figure 2.2 shows the behavioural responses of the three mysid species to the different mixtures of betaine and ammonia. These data include the frequency of food capturing and tail flipping behavioural responses, and animals which did not show any response at all. The response to the different test mixtures by *A. mixta australis* individuals followed the trend: 75:25 > 100:0 > 25:75 > 50:50 = 0:100. However, only those responding to the first three test mixtures were significantly different from the seawater controls (Table 2.1, G-test of independence with William's correction, $p < 0.05$ for all). The response of *P. rufa* followed the trend: 50:50 > 25:75 > 100:0 > 75:25 > 0:100 > seawater control. Except for the 0:100 test mixture, responses to the first four test mixtures were significantly different from the seawater control (Table 2.1, G-test, $p < 0.01$ for all). In *T. tasmaniae*, the response trend to the different test

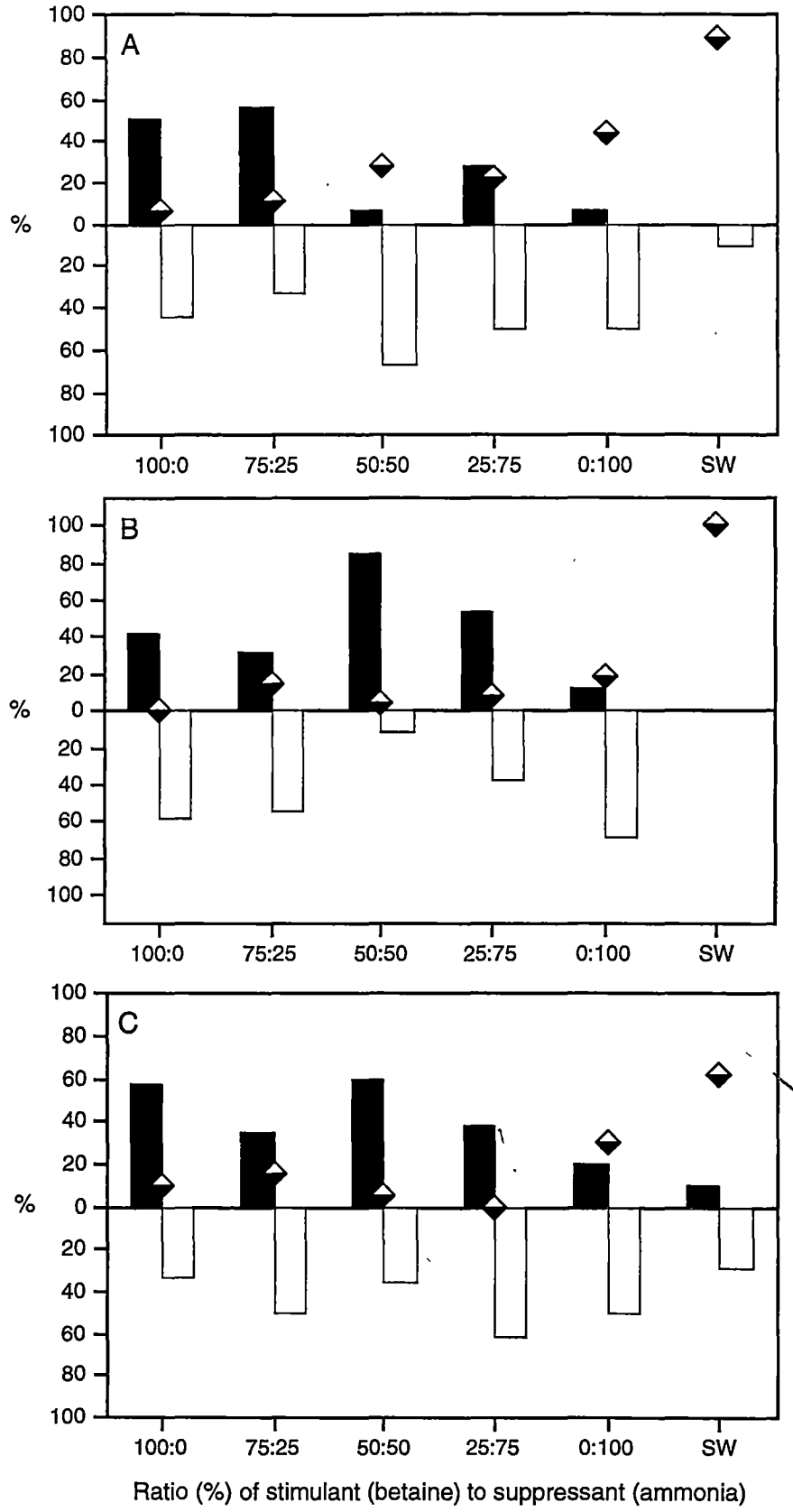


Figure 2.2 Percent responding mysids to mixtures of varying proportions of 10^{-3}M betaine-HCl and 10^{-3}M ammonia. A. *Anisomysis mixta australis*. B. *Paramesopodopsis rufa*. C. *Tenagomysis tasmaniae*. Legend: solid bar - capture response, open bar - tail-flip, half-open and half-solid diamond - no response.

mixtures was 50:50 > 100:0 > 25:75 > 75:25 > 0:100 > seawater control. However, only the responses to 100:0 and 50:50 test mixtures were significantly different from the control seawater (Table 2.1, G-test, $p < 0.01$ for both).

Table 2.1 Food capturing response by the three mysid species to betaine:ammonia test mixtures and to seawater (SW) controls.

Anisomysis mixta australis

Mixture ratio	Proportion	*G* value
100:0	0.50	11.82^{***}
75:25	0.56	13.20^{***}
50:50	0.06	0.92^{ns}
25:75	0.28	6.30^{*}
0:100	0.06	0.92^{ns}
SW	0.00	—

Paramesopodopsis rufa

Mixture ratio	Proportion	*G* value
100:0	0.42	14.59^{***}
75:25	0.31	10.44^{**}
50:50	0.85	29.82^{***}
25:75	0.54	18.74^{***}
0:100	0.12	3.56^{ns}
SW	0.00	—

Tenagomysis tasmaniae

Mixture ratio	Proportion	*G* value
100:0	0.57	7.65^{**}
75:25	0.35	2.79^{ns}
50:50	0.60	7.65^{***}
25:75	0.38	3.67^{ns}
0:100	0.20	0.63^{ns}
SW	0.10	—

df = 1, ns = no significant difference, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$

In all three species, comparable proportions of individuals displayed the capturing behaviour in response to the 100:0 mixture (G-test, df = 2, $p > 0.05$). *Anisomysis mixta australis* and *P. rufa* responded both to 75:25 and 25:75 mixtures, but whereas their response to the former stimulus was comparable (G-test, df = 1, $p > 0.05$), more *P. rufa* than *A. mixta australis* individuals responded to the 25:75 test

mixture (G-test, df = 1, $p < 0.05$). Both *T. tasmaniae* and *P. rufa* responded to the 50:50 test mixture, but the latter species showed a significantly higher proportion of responding individuals than the former species.

Table 2.2 Tail-flipping response by the three mysid species to betaine:ammonia test mixtures and to seawater (SW) controls.

Anisomysis mixta australis

Mixture ratio	Proportion	*G* value
100:0	0.44	3.67^{ns}
75:25	0.33	1.96^{ns}
50:50	0.67	7.65^{**}
25:75	0.50	4.61^{*}
0:100	0.50	4.61^{*}
SW	0.11	—

Paramesopodopsis rufa

Mixture ratio	Proportion	*G* value
100:0	0.58	20.12^{***}
75:25	0.54	18.74^{***}
50:50	0.12	3.56^{ns}
25:75	0.38	13.20^{***}
0:100	0.69	24.28^{***}
SW	0.00	—

Tenagomysis tasmaniae

Mixture ratio	Proportion	*G* value
100:0	0.33	0.07^{ns}
75:25	0.50	0.98^{ns}
50:50	0.35	0.07^{ns}
25:75	0.62	2.57^{ns}
0:100	0.50	0.98^{ns}
SW	0.29	—

df = 1, ns = no significant difference, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$

Tail-Flipping Response

Anisomysis mixta australis tail-flipped in response to all test mixtures and the seawater control. However, only responses to 50:50, 25:75, and 0:100 were significantly different from the seawater control (Table 2.2; G-test, $p < 0.05$). The

highest number of tail-flippings in this species were in response to the 50:50 mixture. Except for the 50:50 test mixture and seawater control, *P. rufa* tail-flipped in response to all other test mixtures (G-test, $p < 0.001$). The highest proportion of tail-flippings were observed in response to the 0:100 mixture, followed by 100:0, then 75:25, and the lowest was in response to the 25:75 mixture. The number of *T. tasmaniae* which tail-flipped in response to the five test mixtures was comparable to those which responded to the seawater control (G-test, $p > 0.05$ for all).

The tail-flippings by *P. rufa* in response to 75:25 and 0:100 test mixtures were greater than those of *A. mixta australis* responding to the same test mixtures.

Response to Glycine:Ammonia Solution

Food Capturing Response

Figure 2.3 summarizes the percentages of responding individuals of the three mysid species to the different test mixtures and seawater controls. Fewer individuals responded to the glycine:ammonia assay than to the betaine:ammonia assay. The proportion of food capturing *A. mixta australis* individuals was greatest in response to the 50:50 test mixture (Table 2.3; G-test, $p < 0.001$). The 100:0 and 75:25 mixtures elicited fewer food capture responses (Table 2.3; G-test, $p < 0.05$). Numbers of *A. mixta australis* individuals stimulated by the 25:75 test mixture were not significantly different from those which responded to the seawater control. This species showed no response to the 0:100 test mixture. The 50:50 was the only test mixture which significantly elicited strong food capturing in *P. rufa* (Table 2.3; G-test, $p < 0.001$). *T. tasmaniae* responded strongest to the 50:50 mixture (Table 2.3; G-test, $p < 0.001$), but fewer individuals of this species showed a significant response to 25:75 test mixture.

The food capturing responses of the three species to the 50:50 mixture were comparable (G-test, df = 2, $p > 0.05$).

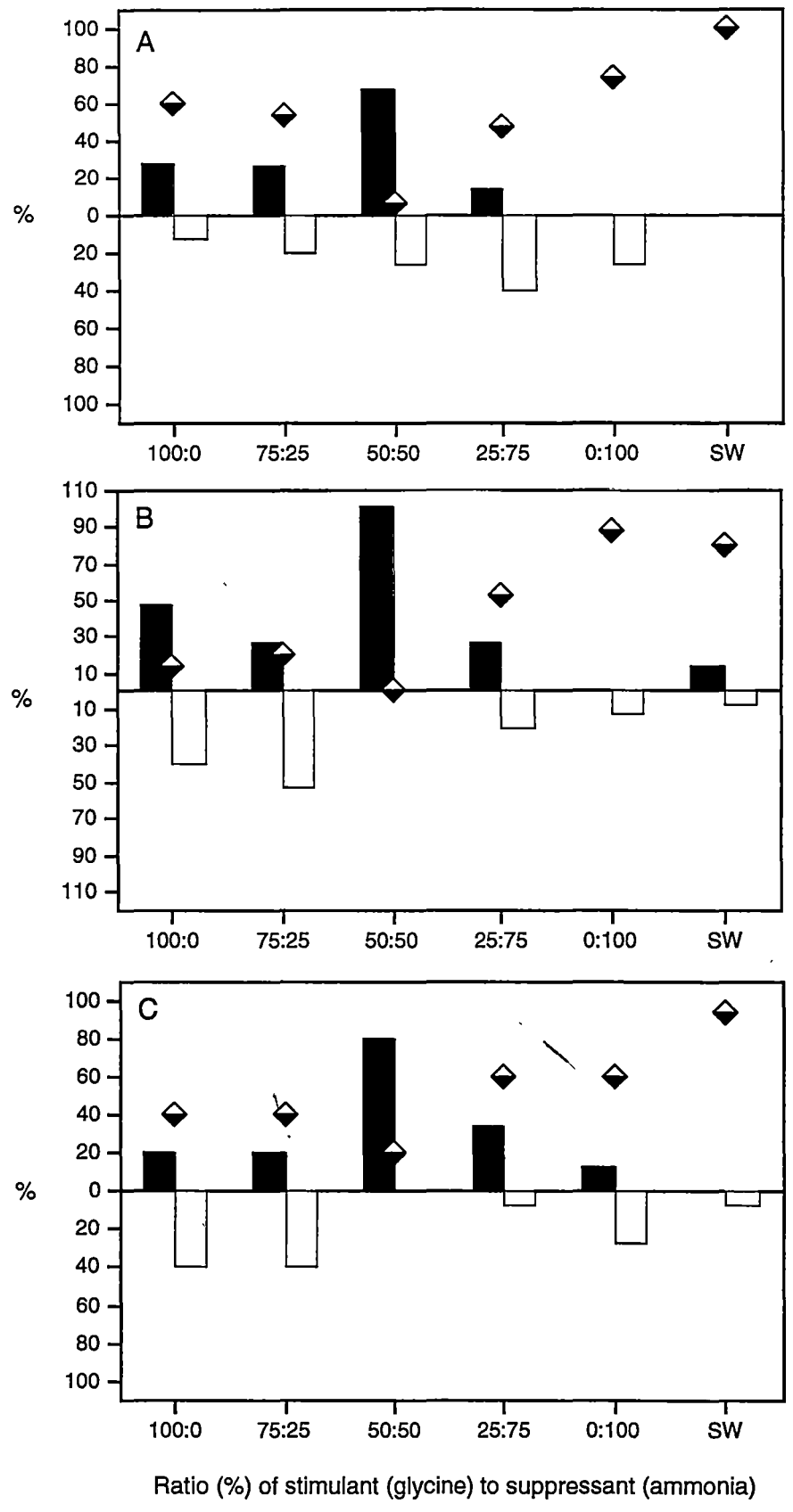


Figure 2.3 Percent responding mysids to mixtures of varying proportions of 10^{-3}M glycine and 10^{-3}M ammonia. A. *Anisomysis mixta australis*. B. *Paramesopodopsis rufa*. C. *Tenagomysis tasmaniae*. Legend: solid bar - capture response, open bar - tail-flip, half-open and half-solid diamond - no response.

Table 2.3 Food capturing response by the three mysid species to glycine:ammonia test mixtures and to seawater (SW) controls.

Anisomysis mixta australis

Mixture ratio	Proportion	*G* value
100:0	0.27	4.93*
75:25	0.27	4.93*
50:50	0.67	13.20ns
25:75	0.13	2.20ns
0:100	0.00	0.00
SW	0.00	—

Paramesopodopsis rufa

Mixture ratio	Proportion	*G* value
100:0	0.47	2.79ns
75:25	0.27	0.63ns
50:50	1.00	10.93***
25:75	0.27	0.63ns
0:100	0.00	0.00
SW	0.13	—

Tenagomysis tasmaniae

Mixture ratio	Proportion	*G* value
100:0	0.20	3.56ns
75:25	0.20	3.56ns
50:50	0.80	15.97***
25:75	0.33	6.30*
0:100	0.13	2.22ns
SW	0.00	—

df = 1, ns = no significant difference, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$

Tail-Flipping Response

The 25:75 and 0:100 test mixtures evoked significant tail flipping responses in *A. mixta australis* (Table 2.4; G-test, $p < 0.05$ for both), while the responses to the rest of the test mixtures were similar to those to the seawater control. Tail-flipping in *P. rufa* was only observed in response to the 75:25 test mixture. In this species, no

tail-flipping response at all was observed to the 50:50 mixture, while the response to the rest of the test mixtures were comparable to those for the seawater control (Table 2.4). The responses of *T. tasmaniae* to 100:0, 75:25, 25:75, 0:100 test mixtures were similar to those in response to the seawater control (Table 2.4).

Table 2.4 Tail-flipping response by the three mysid species to glycine:ammonia test mixtures and to seawater (SW) controls.

Anisomysis mixta australis

Mixture ratio	Proportion	*G* value
100:0	0.13	2.22^{ns}
75:25	0.20	3.56^{ns}
50:50	0.07	0.92^{ns}
25:75	0.47	9.06^{**}
0:100	0.27	4.93^{*}
SW	0.00	—

Paramesopodopsis rufa

Mixture ratio	Proportion	*G* value
100:0	0.40	3.70^{ns}
75:25	0.53	5.87^{*}
50:50	0.00	0.00
25:75	0.20	0.93^{ns}
0:100	0.13	0.29^{ns}
SW	0.07	—

Tenagomysis tasmaniae

Mixture ratio	Proportion	*G* value
100:0	0.40	3.70^{ns}
75:25	0.40	3.70^{ns}
50:50	0.00	0.00
25:75	0.07	0.00
0:100	0.27	1.75^{ns}
SW	0.00	—

df = 1, ns = no significant difference, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$

Discussion

Response to Betaine-HCl: Ammonia

It is highly likely that betaine-HCl speciates into other forms in seawater; the rate of change is obviously dependent on many physical parameters. To my knowledge, no study has examined the behaviour of this tertiary amine in seawater. The response shown by the mysids is the summation of betaine interactions with the other compounds in solution.

Anisomysis mixta australis

More food capturing responses by *A. mixta australis* occurred at 100% and 75% betaine-HCl. The 50:50 or 1:1 mixture, in contrast, evoked the highest fleeing response. The capturing response of *A. m. australis* to high levels of betaine-HCl might be parallel to those observed in lobsters. Taste receptors in various feeding appendages of lobsters maintain their function even at high stimulus concentration such as those the lobster's legs encounter during natural feeding (Johnsson *et al.* 1984; Borroni *et al.* 1986; Derby and Atema 1988).

Although capturing responses were significant at 25:75 test mixture, higher proportions of equally significant tail-flips suggest that the results could be interpreted as more of a suppression effect by ammonia. This further implies that mixtures of stimulant and suppressant result in a combination of feeding and fleeing responses in which one or the other will dominate depending on other circumstances. Ammonia alone, however, exerted a feeding inhibitory effect, as evidenced by tail flipping and/or fleeing response by *A. m. australis*.

Ammonia is one of the most common excretory products in aquatic organisms (Zimmer-Faust 1987). In lobsters, for example, it may be used as a food identifying compound, and at high concentrations it may become toxic and inhibitory to clasping behaviour (Fuzessery and Childress 1976; Carr and Derby 1986; Zimmer-Faust 1987). The ratio between stimulatory and suppressive effects of ammonia may

dominate behavioural responses of organisms being studied (Borroni *et al.* 1986). For instance, Bainbridge (1953) noted that in *Hemimysis lamornae*, ammonia at 10^{-3} M concentration was an attractant, and this compound may serve as a cue for aggregation in this group of crustaceans. Zimmer-Faust (1987) noted that under some conditions ammonia is chemoattractive depending on the organisms using it as a cue specific to their preferred food. Scavenging animals and detritivores are often found attracted to ammonia (Zimmer-Faust 1987, 1989). Borroni *et al.* (1986) noted that only ammonium chloride (NH_4Cl) was stimulatory at the behavioural level of the ablated lobster chela which possesses an abundant population of narrowly tuned receptor cells.

In *A. mixta australis*, the tail-flippings in response to the 1:1 test mixture and more food capturing responses to the higher concentrations of betaine-HCl indicate that fresher tissues from animal prey may be preferred by this species compared to the other two species. Higher levels of food capturing are cued by relatively higher betaine concentrations resulting in the species bell-shaped response curve being more skewed to the left.

Paramesopodopsis rufa

The dominance of tail-flipping in response to 100% betaine-HCl and 75:25 test mixtures over food capturing response clearly demonstrates the suppression effects of high levels of betaine-HCl on feeding behaviour. This is a similar phenomenon to that shown in other predatory or scavenging marine crustaceans (Carr and Derby 1986). *Paramesopodopsis rufa* responded to the unusually high levels of betaine-HCl with escape behaviour suggesting that perhaps the animal requires the optimal proportion of both "suppressant" and "stimulant" for stimulating the right proportion of both betaine-HCl and ammonia gustatory receptors. Stimulation of mainly betaine-HCl receptors may result in negative messages to neural centres and cause the animal to flee.

In *P. rufa*, the ideal or optimal proportions of both feeding suppressant and stimulant is unequivocally demonstrated by the dominance of food capturing response

to the 1:1 test mixture. This is apparently true of the 25:75 test mixture as more capturing response than tail flippings were displayed. It is interesting to note that despite the already high concentration of ammonia, the 25% contribution of betaine-HCl to the mixture results in more food capturing response. Recently, Harpaz and Steiner (1990) noted that betaine-HCl overrules all chemical feeding stimulants in the test solution used.

The dominance of the feeding suppression effects of ammonia is clearly shown in the 0:100 test mixture. This observation is not new; studies on crustaceans from different phylogenetic groups (Zimmer-Faust et al. 1984, 1987; Carr 1988; Strand and Hamner 1990) and fish (Carr 1988) produced similar responses to high levels of ammonia.

The overall response of *P. rufa* to the test mixtures can be summarized as a bell-shaped curve with suppression effects at high levels of betaine-HCl and ammonia while optimal food capturing occurs in response to equal proportions of the two compounds.

Tenagomysis tasmaniae

Tenagomysis tasmaniae displayed similar capturing responses to those of *A. m. australis* when tested with the 100:0 mixture and similar explanations are proposed. The response of this species to the 75:25 test mixture is similar to that shown in *P. rufa* and thus may be similarly explained. However, because the tail-flipping responses to the 75:25 test mixture and the seawater control (control 1) were similar, this deduction is tentative. The latter result could be attributed to the very high variability in responses of *T. tasmaniae* individuals to the test mixtures. These results suggest two things: the first is that seawater alone could elicit both capturing and tail-flipping behavioural responses, and the second is that *T. tasmaniae* is more sensitive than the other species to laboratory conditions. The first suggestion is supported by similar conflicting results in other crustaceans (Zimmer-Faust 1987). *Tenagomysis tasmaniae* may have interpreted seawater introduction as a sudden rush of food-laden current, thus food capturing behaviour was shown. This could be an adaptation in

mysids which position themselves to face water currents which are laden with food particles. In contrast, a sudden rush of seawater may be interpreted as danger, resulting in tail-flips.

Similar mechanisms to those proposed in *P. rufa* may explain the high capturing response to the 50:50 test mixture by *T. tasmaniae*. Although suppression effects were shown in response to 25:75 and 0:100 (high levels of ammonia) test mixtures, this may just be apparent because the tail-flips in response to these mixtures were insignificantly different from those in the seawater controls. The flatter bell-shaped response curve of this species may not be valid for this reason.

Response to Glycine:Ammonia

Zimmer-Faust *et al.* (1984) noted that neither ammonia nor urea binds with glycine, thus response by the three mysid species should not be obscured by the possible speciation and interaction of these compounds once in contact with seawater.

All three species showed similar optimal capturing behavioural response to the 50:50 glycine:ammonia mixture. This indicates that the optimal combination of both suppressant and stimulant is similar to that for *P. rufa* and *T. tasmaniae* when responding to the betaine-HCl:ammonia mixture. The suppression effect brought about by high concentration levels of stimulants is again clearly demonstrated in the glycine:ammonia assay.

Implications

The similar bell-shaped chemosensory response pattern shown by both *P. rufa* and *T. tasmaniae* to the mixtures of betaine:ammonia, and similar response patterns of the three species to glycine:ammonia mixtures, to some extent , probably reflect shared trophic ecologies of the three species (Weissburg and Zimmer-Faust 1991). Similarity of response to the same test mixtures is an indication that similar types of chemoreceptors are shared in the three mysid species. Abundance and distribution of

these receptors, and the mechanisms they regulate may, nonetheless, vary between the three species. However, a more pointed bell-shaped (leptokurtic) curve for *P. rufa* (and a more stereotyped feeding behavioural response) compared to that in *T. tasmaniae* , suggests a higher affinity of *P. rufa* for betaine-HCl than is the case with the former species. This could be related to differential utilization of betaine-HCl rich food materials such as decomposing and fresh animal tissues. *Paramesopodopsis rufa* has been regarded as primarily carnivorous as indicated by the relatively high proportion of crustacean remains in its stomachs (Fenton 1986). The indistinct response pattern by *A.m. australis* is more of a reflection of suppression effects by chemical mixtures and their concentration. This could well be related to the fact that the concentration levels of both chemo-stimulant and -suppressant used in the present study may be highly suppressive resulting in negative feeding behavioural response (Zimmer-Faust *et al.* 1984, 1987; Carr and Derby 1986; Derby and Atema 1988).

To my knowledge, this is the first study on the gustatory aspects of feeding in three co-occurring mysid species. Both similarities and differences in optimal chemosensory feeding responses were observed in the three species. These differences, superimposed on and interacting with other ecological circumstances, may serve as a mechanism by which feeding niche partitioning is achieved.

CHAPTER 3

FINE PARTICLE FEEDING MECHANISMS

Introduction

Feeding Mechanisms

Understanding the actual feeding mechanisms in animals is important as it may help elucidate tropho-dynamic processes (Attramadal 1981). High-speed micro-cinematographic observations reveal that feeding mechanisms in calanoid copepods resemble neither filtering nor sieving (Alcaraz *et al.* 1980; Koehl and Strickler 1981; Strickler 1982; Price *et al.* 1983; Glasser 1984; Koehl 1983). A copepod captures and rejects particles actively by flinging the maxillae open and then drawing them closer to the body. Their appendages act more like a paddle than a rake because of the highly viscous physical world as experienced by objects at low Reynolds number (*Re*). These appendages cannot passively sieve particles nor allow particles to adhere because a relatively thick boundary layer of water adheres to the primary setae and secondary setules; particle movement and water flow stops when the copepod stops beating its appendages (Koehl and Strickler 1981; Strickler 1984). Capture of particles is achieved by the asymmetric movements of the appendages sucking particles toward the mouthparts. These studies have given impetus to research on mechanical and chemical cues that determine selective feeding (Koehl and Strickler 1981) and the diversity of feeding behaviour of zooplankters (Paffenhøffer 1988).

A clearer picture of the filter feeding process in *Euphausia superba* has been reported in a study by Hamner (1988). Using high-speed color photography (at 24-64 frames s^{-1}), Hamner has resolved previous conflicting views (Lebour 1924; Barkley 1940, cited in Jørgensen 1966; Mauchline and Fisher 1969; Berkes 1975). He showed that *E. superba* filter-feed by the compression pumping of the food basket which is formed by the elaborately setose endopods of the pereiopods. Water containing food particles is sucked in and then compressed by the endopods which

expels water laterally and simultaneously traps the food inside the basket. The exopods cover the sides of the feeding basket thereby improving the valving action of the basket. A food bolus is formed, which is pressed by the mandibular palps against the mandibles, and is ingested.

Mysids capture and process large food particles using their multi-articulate pairs of endopods (Depdolla 1923; Cannon and Manton 1927; Mauchline 1980; Crouau 1989). However, reports on the feeding mechanism employed to capture fine food particles are contradictory. Depdolla (1923) stated that posteriorly directed ventral currents bear fine particles which are scooped up by the maxillae and the maxillipeds. According to Cannon and Manton (1927) *Hemimysis lamornae* capture fine food particles via exopod "axial" currents which unite into a ventral food groove current drawn anteriorly by some suction mechanisms of the mouthparts. Berkes (1975) noted that in the large (40 mm) *Boreomysis nobilis* the ventral currents created by the exopodites pass between the two rows of thoracic appendages and not between the two bases of adjacent limbs. Attramadal (1981), however, reported that ventral filtration currents described in the two previous studies were experimental artefacts due to the small volume of water in which the animals were submerged. Recently, Schabes and Hamner (1992) reconfirmed the findings of Depdolla (1923) that mysids collect food from the front, and reported that Cannon and Manton's exopod axial currents do not exist.

Attramadal (1981) noted that mysids gather and eat food particles adhering on setae and the body surface by various "cleaning movements" (grooming behaviour), an observation similar to those reported in intertidal amphipods (*e.g.* Sheader and Evans 1975; Robertson and Mann 1980; McGrouther 1983). Apart from Attramadal's study, grooming behaviour and its role in mysid feeding behaviour have not been reported. However, a recent study by Acosta and Poirrier (1992) noted the importance of grooming behaviour in ridding fouling agents from the surfaces of the mysid exoskeleton.

Particle Size Selection

The pelagic zone of the sea contains suspended organic and inorganic particulate material. The particulate organic matter (POM), which occurs in a spectrum of sizes and shapes, provides energy and nutrients in the pelagic zone (Angel 1984). The term 'seston' has been used to refer to all particulate material, both living organisms (plankton) and detritus (Parsons *et al.* 1984). Sieburth *et al.* (1978) proposed the scheme below based on size categories of the plankton:

Size category	Taxonomic category		Size
femtoplankton	(virioplankton)	-	0.02 to 0.20 μm
picoplankton	(bacterioplankton)	-	0.20 to 2.00 μm
nanoplankton	(myco-, phyto-, and protozooplankton)	-	2.00 to 20.0 μm
microplankton	(phyto-, and protozooplankton)	-	20.0 to 200 μm
mesoplankton	(metazooplankton)	-	0.20 to 20.0 mm
macroplankton	(centimetre nekton)	-	2.00 to 20.0 cm
megaplankton	(decimetre nekton)	-	20.0 to 200 cm
	(meter nekton)	-	2.00 to 20.0 m

Suspension feeding is an abstraction of different sized suspended food and non-food particles by food handling appendages (Jørgensen 1966). Suspension feeding organisms have had to evolve a variety of ways of maximizing the chances of exploiting these small and frequently widely dispersed particulate food resources (see Jørgensen 1966; Conover 1981; Barnes *et al.* 1988, pp. 273-296). According to Price (1988), particle size selection may operate in each of the different components (*e.g.* encounter, pursuit, capture and ingestion) of the feeding mechanisms in zooplankton. The five possible methods of particle capture proposed by Rubenstein

and Koehl (1977) (direct interception, inertial impaction, gravitational deposition, diffusion or motile particle deposition, and electrostatic attraction) may have determined the diversity of suspension feeding modes (*e.g.* setose filtration, mucus-bag and mucus sheet suspension feeding, ciliary mucus mechanism (Levinton 1982)) in a variety of organisms. Size of particles ingested may serve as a niche axis in which species partition resources and which may consequently promote co-occurrence (Fenchel *et al.* 1975; Taghon 1982).

A number of studies have been devoted to particle size selection which has direct implications for feeding niche separation. For example, studies on particle size selection in suspension feeders have been undertaken using algal cultures (*e.g.* Frost 1972, 1977; Gaudy 1974; Koehl and Strickler 1981), naturally occurring phytoplankton (*e.g.* Poulet 1978; Cowles 1979; Bartram 1980), combination of cultured and natural population of phytoplankton (*e.g.* Nival and Nival 1976), inert particles (*e.g.* Wilson 1973; Donaghay and Small 1979; Gophen and Geller 1984; Miller 1984; Okamura 1990; Zankai 1991), and combinations of inert particles and algal cultures (*e.g.* Donaghay and Small 1979; Bern 1990). A full understanding of patterns of feeding selectivity requires emphasis on particle characteristics other than size, *e.g.* taste, motility, food value, concentration, and surface chemistry (Okamura 1990). Food acclimation or pre-conditioning (Donaghay and Small 1979), the ability to alter parts of their food handling appendages, in particular the setal systems of the mouthparts, and scanning and location of larger and more efficiently handled and ingested particles (Wilson 1973) may influence copepod food size selection. Suspension feeding on inert beads in two species of bryozoans is also influenced by ambient water flow velocities (Okamura 1990). Furthermore, post-capture rejection mechanisms may determine the preferred food particle size (Miller 1984; Donaghay 1988). An obvious advantage in using inert and uniform shaped particles is that variables associated with shape and palatability may be eliminated (Wilson 1973: Miller 1984). However, inherent in these studies is the fact that the animals do not normally feed on plastic beads.

Aims

The conflicting versions of mysid feeding mechanisms may be a reflection of the fact that different species show modifications which are very subtle. In this study, the differences in feeding behavioural responses of the three co-occurring mysid species to various food and non-food suspensions were examined using micro-videography. In particular: (1) the limb postures associated with the collection of fine food particles and with grooming behaviour, and (2) movements of fine food particles around the cephalothoracic appendages, are compared in these mysid species.

No study which is aimed at understanding aspects of feeding mechanisms in mysids has been done using plastic beads. In the present study, feeding trials on inert plastic beads by the three co-occurring mysid species were conducted in order to derive insights into particle size selection aspects of suspension feeding in these animals.

Materials and Methods

Microvideographic Observation of Feeding Behaviour

The field collection and laboratory maintenance of the three species of mysids are described in detail in chapter 2. The filming set-up used in the observation of feeding mechanisms in response to food and inert beads suspensions has also been described in chapter 2. Different suspensions made of iodine-stained starch grains, freshly prepared mysid homogenate, mashed fish pellets, and < 63 μm (longest dimension) ground brown alga (*Lessonia corrugata*) were supplied as food particles. These foodstuffs were introduced consecutively in front of a tethered animal using Pasteur pipettes in amounts just sufficient to elicit changes in the posture of thoracic endopods.

A similar concentration of beads used in the feeding experiment with free swimming mysids (see below) was used to observe the movements of feeding appendages in response to the mixture of beads. The bead suspension was introduced approximately 1 cm in front of a tethered mysid by squirting slowly 1 mL of suspension from a Pasteur pipette.

A total of six adult individuals of each species (3 males and 3 females) were observed. In order to get a 3-dimensional view of the various feeding behavioural responses, subjects were viewed from different angles. After filming, the animals were detached from their tethers and immediately killed in hot tap water. Dead mysids were then preserved in 5% (v/v) formalin in filtered seawater. In order to confirm bead ingestion, the stomachs of these test animals were dissected out, teased apart and mounted on glass slides with polyvinyl lactophenol (PVL) and covered with glass cover slips. The videotapes were viewed three times to confirm behavioural response.

Laboratory Feeding Experiments

Experiments on selection of different sizes of plastic beads by mysids were conducted with the three mysids species held separately. This was necessary to avoid cannibalism which occurred when all three species were combined in one feeding chamber. The larger *P. rufa* and *T. tasmaniae* species attacked and usually removed the eyes of the smaller *A. mixta australis*. More often, *T. tasmaniae* attacked both active and dying *P. rufa* individuals and *vice versa*. The experiment comprised 10 replicate samples, each of which was a jar containing a 2-L suspension of mixed beads and six mysids. Two control samples which contained a similar volume and concentration of bead suspension and six head-squeezed mysids, to account for any non-feeding bead losses, were run concurrently with the replicate samples.

Prior to the feeding experiments, animals from the holding tank were transferred to 10-L aquaria containing 5 μm Millipore-filtered seawater for 24 h to allow complete gut clearance. To verify gut clearance, foreguts were dissected out

from randomly selected individuals, and with the use of micro-dissecting forceps, each foregut was cut on its dorsal region, teased apart, and mounted in PVL. Examination of guts was completed using a Nikon phase contrast microscope at 100X and 200X magnifications.

Five colour-coded size classes of plastic beads (Ionics, Inc.: Watertown, Massachusetts) (10-20 μm, 20-30 μm, 30-40 μm, 50-60 μm, and 80-90 μm) were used. The average (± SD) sizes for each bead type were measured, and they were coded I (11.95 ± 2.45 μm), II (20.72 ± 3.15 μm), III (36.73 ± 5.50 μm), IV (64.98 ± 6.36 μm), and V (90.23 ± 9.78 μm) for convenience. Prior to preparation of the stock suspension, the beads were washed in distilled water, and the two smallest size ranges were sonicated for 15 s to disaggregate any clumps. Volumes of stock suspension of known concentration were added to 2-L polyethylene jars, to obtain final concentrations of approximately 3000 to 5000 beads mL^{-1}. To determine the concentration of each size category of plastic beads before and after a feeding experiment, 1 mL of the plastic bead suspension was filtered on a 0.45 μm Millipore membrane filter (2.5 cm diameter). Retained beads on the filter were counted at 100X and 200X magnifications under a compound microscope. During counting, diameter of beads was always verified using the ocular micrometer since colour codes of beads were indistinguishable. The average count of beads from five randomly distributed microscopic fields was obtained and multiplied by a conversion factor to obtain number of beads mL^{-1}.

To start a feeding experiment, six individuals of similar length were transferred into a jar containing beads, and allowed to feed for 20 min, a period shorter than the average time for gut passage of particles (Murtaugh 1984). In order to keep the plastic beads in suspension, the jars or feeding chambers were tightly wrapped in aluminium foil and rolled horizontally on a "plankton roller" (Omori and Ikeda 1984) at an average of 0.83 revolutions min^{-1} ± 0.2 SD. The entire feeding experiment was conducted under dim light, and water temperature was 13 °C. After each 20-min experiment, the animals were removed from suspension and killed by plunging them into hot water. In this manner, regurgitation of stomach contents is

prevented (Wilson 1973). Dead animals were preserved in 4% (v/v) buffered formalin in filtered seawater for subsequent analysis. Before dissection, the total lengths of individual mysids were measured from the anterior tip of the carapace to the posterior tip of the telson (excluding the setae) under a dissecting microscope with calibrated graticule attached to the eyepiece. Removal and dissection of guts from individual mysids followed the same procedure as in the verification of gut clearance. All ingested beads found in the guts were counted using a phase contrast compound microscope at 200X magnification for the smaller particles and at 100X magnification for the larger ones.

Data Analysis

Bead counts from the guts of six individuals were pooled to represent a replicate value of ingested beads, while the concentration of beads mL^{-1} from each replicate jar served as the beads available for ingestion. The selection for the different size classes of available beads was calculated using Ivlev's Electivity Index formula:

$$E = [Ri - Pi]/[Ri + Pi],$$

where i = particle of a given size range; R = the proportion of total beads ingested; P = the proportion of available beads. The volume of seawater cleared of all sizes of beads (clearance rate in μl $mysid^{-1}$ h^{-1}) of the three species of mysids was calculated using the formula (P-Zankai 1992):

$$CR = [B \times 60]/[C \times T],$$

where B = number of all beads or number of beads in any size class in the guts; C = number of all beads in 1 mL of suspension; T = incubation time (20 min). The ingestion rate of beads expressed as the number of beads ingested $mysid^{-1}$ hr^{-1} was also determined for each mysid species. The data from the three species were analyzed using one-way analysis of variance (ANOVA) followed by a post hoc comparison of means using the Tukey's Honestly Significant Difference test to determine which means differed significantly. All statistical analysis was carried out using the SYSTAT software for Macintosh computers (Wilkinson 1992).

Results

Feeding Mechanisms

Videotapes of the different behaviours described here are lodged in the Department of Zoology, University of Tasmania.

Paramesopodopsis rufa Fenton 1985

Pre-Food Introduction Observations

Currents can be observed by tracing the motion of algal particles. All particles were directed backwards. Currents coming from many directions can be seen approaching the anterior region of the animal. In *P. rufa*, the vigorous metachronal motion of exopods caused adpressed individual endopods to oscillate; this was more apparent in the lower three podomeres (dactylus, propodus and carpus) of the endopods than in the upper podomeres (merus and ischium).

The lateral view of the animal with adpressed endopods and exopods rapidly moving exhibited a streamlined body shape as traced by the particle laden fluid flowing around it. The antennal scales and associated structures projected forward and this positioning explains why, looking from the anterior view, these structures can hardly be seen. The shape of the upper half of the animal is like a fuselage to which the antennal scales are anteriorly attached. Viewing the different angles of a streamlined *P. rufa* revealed no front and rear opening that leads to the insides of the adpressed endopods. Nor are there lateral openings since the ischia of the retracted individual endopods were tightly adpressed to each other. At the front, however, intermeshing of the setae projecting from the lower podomeres of the endopods are observed.

Stereotyped Feeding Responses

"outstretching"

"Outstretching" is a series of endopod movements which took about 500 ms, and was initiated by the last pair of endopods. The endopods were first swayed laterally placing the limbs perpendicular to the side of the carapace (Fig. 3.1A). The setae on the medial surface of these spread limbs apparently project ventrally. This is then followed by the thrusting of the limbs forward, which was associated with the ventral pushing motion of the lower half of the body bringing the entire thoracic region more anterior. Either movements of other limbs (described below) or return of the limbs to the original adpressed position came after outstretching. Outstretching which may be performed by either or both left or right side of endopods appeared to generate a current resulting in turbulent vortices of the homogenate in the median region of the underside of the thorax, thus bathing the mouthparts with food particles carried by the current.

"feeding bout"

A "feeding bout" is characterized by the frequent ventral and full stretching of all endopods followed by a series of rapid movements of these appendages as if processing clouds of food particles. Slow motion of these endopod movements reveals the basic crustacean "fling and clap" (*sensu* Weis-Fogh 1973 cited in Strickler 1984) limb movements (Fig. 3.1B). This behaviour was often induced by the fish suspension and mysid homogenate, and often followed by the "outstretching" and grasping modes of the endopods. Endopods performing a feeding bout usually remained stretched and vigorously flinging and clapping for as long as mysid or fish suspension bathed these limbs. The rapid ventral stretching of endopods in a feeding bout appeared to suck the food suspension towards the mouth region as in "outstretching". During the feeding bout, the lowering and ventral stretching of endopods varied in angles (c. 20°-50° range) relative to the horizontal axis of the ventral region of the thorax.

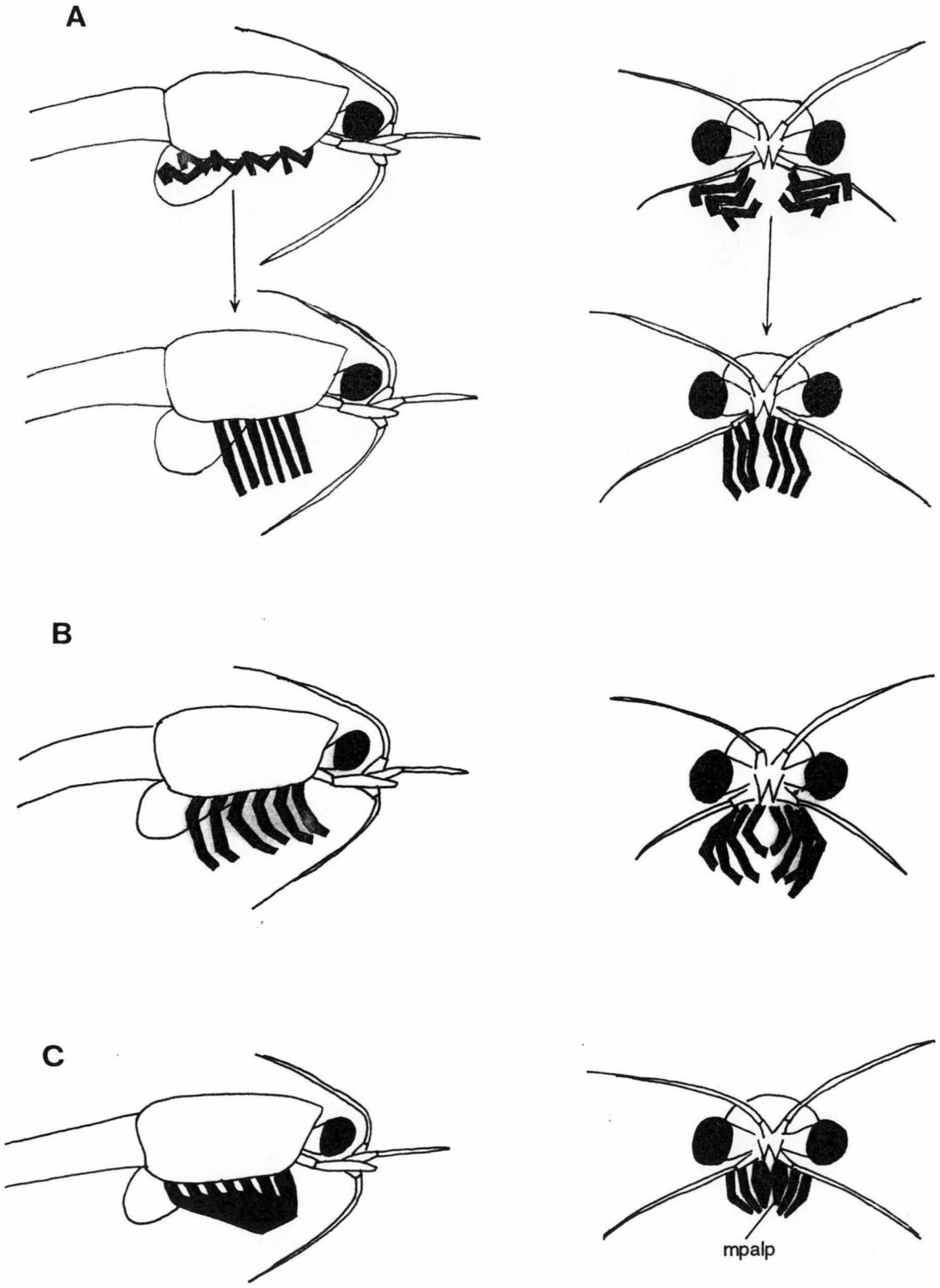


Figure 3.1 Schematic drawings of the different stereotyped thoracic endopod (shaded black) postures. Drawings on the left are lateral view of the anterior half of a mysid, while those on the right are anterior view. A. Outstretching: arrows mean direction of posture sequence. B. Feeding bout. C. Cage formation: mandibular palp (mpalp) as anterior cover (see details in Fig. 3.2).

"cage" formation

"Outstretching", "feeding bout", and grooming behaviour may be followed by "cage" formation (Fig. 3.1C). In this behaviour, the endopod dactyls are brought anteriorly meeting the lowered mandibular palps to form a cage. The cage from the ventral view appeared like a pear-shaped basket with its broader region covering the mouthparts. The cage was composed of two pairs of maxillipeds, the maxillae, the maxillules, the mandibles, and the upper lip or labrum (Fig. 3.2). Inside the cage the first and second pair of maxillipeds vibrated. The first pair of maxillipeds face each other in the mid-ventral region and form a heart-shaped structure through which setae from each podomere project. With their spoon-shaped dactyls, the second pair of maxillipeds were situated ventral to the heart-shaped first pair of maxillipeds. The second pair of maxillipeds displayed a periodic paddling motion. The mandibles showed rhythmic chewing movements during and after cage formation. It appears that food processing and subsequent ingestion probably occurs during cone formation.

Grooming Behaviour

The antennules were regularly groomed. Grooming started with the out-spreading of endopods originating from the hindlegs, followed by the forwardly directed and outstretched endopods which grasped the ventrally flicked (in a whip-like manner) antennae. The exopods, normally beating, were adpressed on the sides of the ischia of endopods during grooming. The antennal scales and flagella swayed laterally upon lowering of the antennules, and remained folded while the antennular cleaning took place. The antennules were also groomed by the combing action of the setose mandibular palp dactyls, and as the antennules slid along the setose inner margin of the antennal scales. Antennular grooming was often performed twice at an interval of about 320 ms.

The three lower podomeres of the endopods, particularly those of the last 2-3 pairs, groomed the antennal scales. The antennal scales and flagella were lowered towards the mid-ventral region of the thorax and grasped by these endopods. SEM

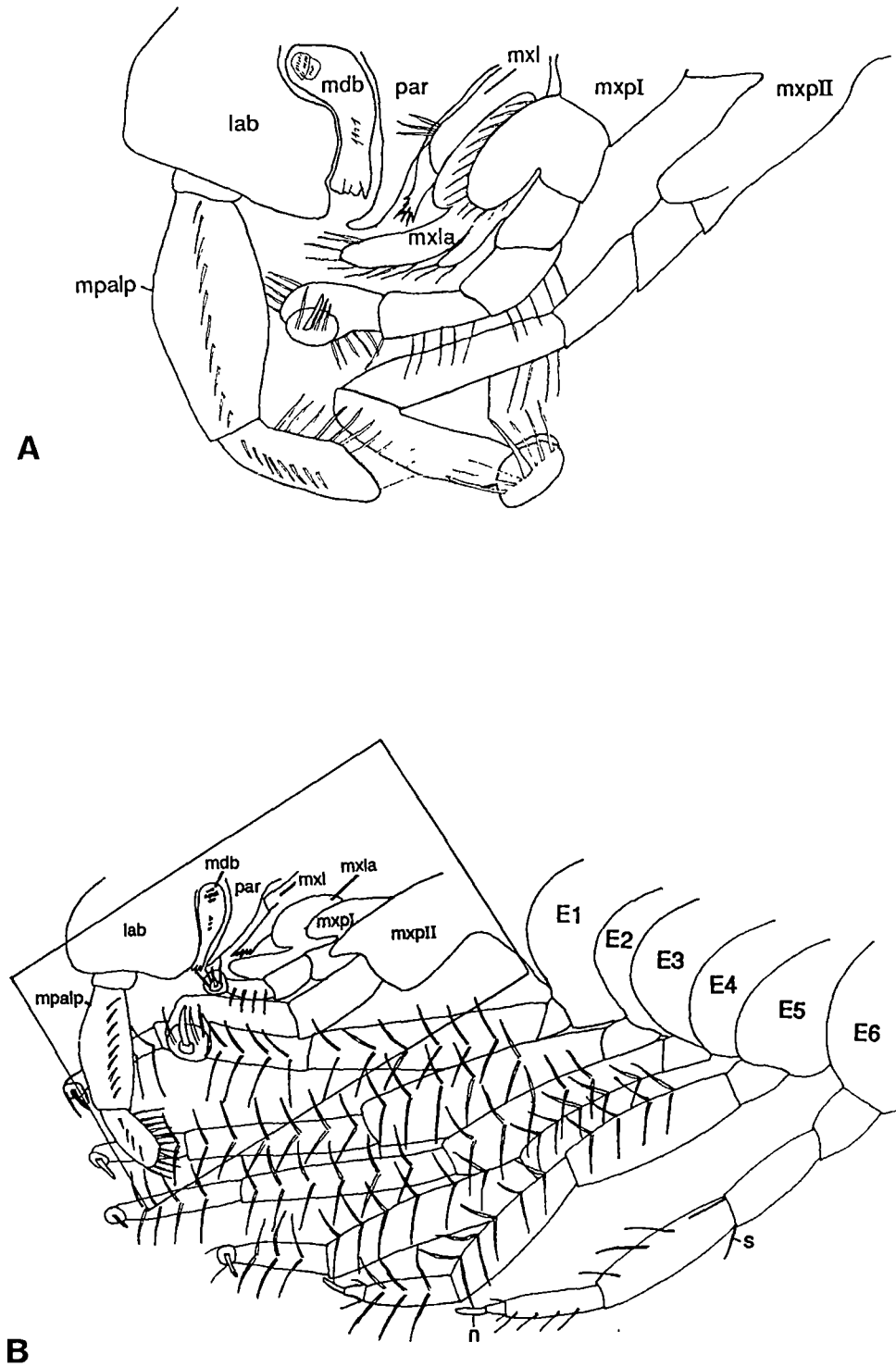


Figure 3.2 A. Lateral view of the inner right half of the primary cage. B. Lateral view of the inner right half of both primary (enclosed in a rectangle) and secondary cages. Abbreviations: E - endopod, lab - labrum, mdb - mandible, mxl - maxillule, mxla - maxilla, mxpI - first maxilliped, mxpII - second maxilliped, n - nail, par - paragnaths, s - seta.

photographs of the lower three podomeres of the endopods showed serrato-dentate setae which probably have a major role in this grooming behaviour (Fig. 3.3; chapter 8: Fig. 8.6D, Fig. 8.7D).

Grooming of the antennules and the antennae was followed by the "cage" formation during which the mandibular palps may be groomed. The mandibular palps were often groomed by the lower podomeres of the endopods after the palps were lowered postero-ventrally. These appendages were also groomed as they rubbed against parts of the antennules and antennal scales and flagella. In addition, they performed autogrooming as often as other mouthparts and pairs of endopods do.

Anisomysis mixta australis Zimmer 1910

The antennal scales and associated structures were groomed or cleaned in a similar manner as in *P. rufa*. A dense cloud of algal particles bathing the endopods were either kicked ventrally or directed ventral to the animal and then backwards by the rapid exopod metachronal motion.

Adpressed to the underside of the thorax, individual endopods vibrated regularly. Either partial or full outstretching was shown by these limbs. The lower podomeres of the endopods can actually be seen picking, in a "chopstick" manner, particles in their vicinity. A stream of stained starch particles bathing the endopods can elicit an intense feeding bout. Although these stereotyped endopod movements in *A. mixta australis* took almost the same length of time as in *P. rufa*, differences in the orientation and positioning of limbs were apparent. When the endopods were brought ventrally (after the initial series of movements described above in *P. rufa*), these limbs were fully bent ventrally and can even reach a perpendicular position relative to the longitudinal axis of the body. In addition, the endopods stayed in this position much longer compared to the same movement in *P. rufa*.

Tenagomysis tasmaniae Fenton 1991

Vibrating due to the rapid motion of the exopods, the last 4 pairs of endopods remained stretched latero-ventrally in an oblique position. Maxilliped II, the third

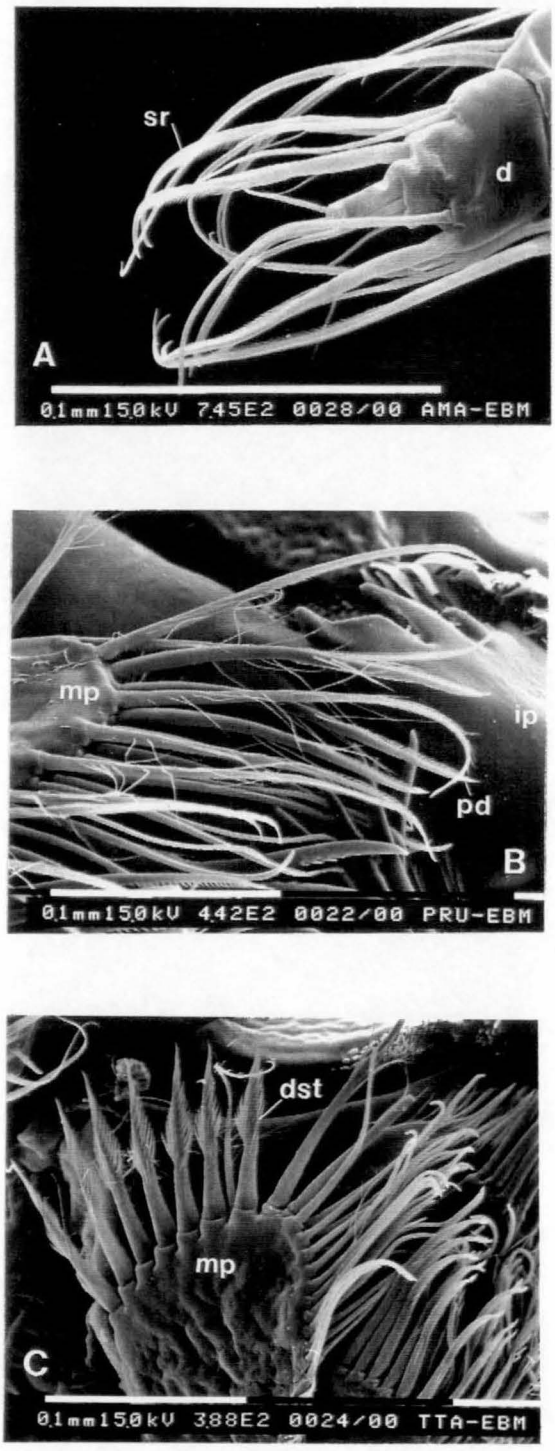


Figure 3.3 Grooming setae of the three mysid species. A. *Anisomysis mixta australis*: sr - serrulate seta, d - dactylus of endopod 1. B. *Paramesopodopsis rufa*: pd - pinnate denticulate seta, mp - maxillary palp, ip - pars incisiva of the left mandible. C. *Tenagomysis tasmaniae*: dst - double-serrated seta, mp - maxillary palp.

and often the fourth pairs of endopods were adpressed to the outer face of the sternal plates of the thorax.

Grooming of antennal scales was similar to that in *P. rufa*, *i.e.* the antennal scales were brought ventrally and groomed by the first and second endopod. The ventrally stretched pairs of endopods can also move towards the underside of the thorax while the exopods were in rapid metachronal motion. A stream of stained starch particles approaching the mid-ventral area of the thorax was seen split into two by the strong exopod backward currents. Particles moving along either sides of the subject were seen bumping the individual endopods, and some particles passed through spaces between two adjacent individual endopods. Particles drawn upwards toward the mouth region were collected by the mouthparts. Independent movements of individual endopods were observed which became particularly apparent in their lower three podomeres. This pair of endopods flung open bringing the particles (size range = 50-70 μm) in between them, and further through suction they were directed towards the maxillae and endopods. The maxillipeds II actively scoop particles bringing them towards the first endopod and the area of the maxillae area.

Feeding Behaviour Involving Inert Bead Particles

Bead Capture, Processing and Ingestion

Observations were similar in the three mysid species. The introduction of beads resulted in either cessation of the exopod movements or the sudden outstretching of endopods and lowering of the mandibular palps. Capture of particles is either from the front or ventral region of the animal. Associated with outstretching of the adpressed endopods, was the erection of their setae by intrinsic muscles, trapping beads on setal surfaces. The fling and clap (Fig. 3.4) movements of the three lower podomeres of the endopods transported particles to the mouth region. Particles were serially transferred by the setae on the first endopods to the mouthparts. The scooping action of maxilliped II helped bring particles to the

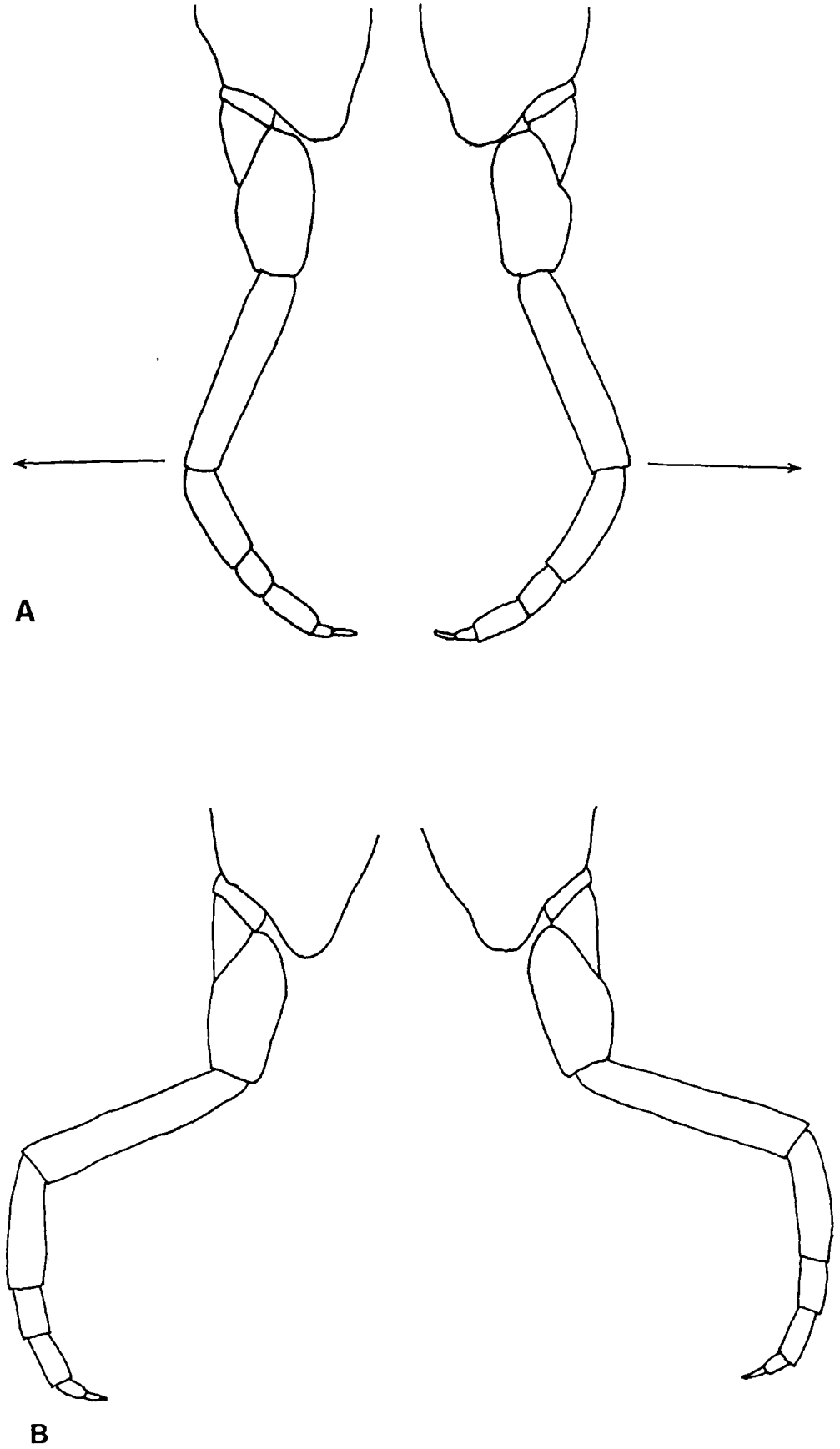


Figure 3.4 Schematic illustration of the "clap" (A) and "fling" (B) movements of the thoracic appendages. Arrows in A represent direction of the flinging movement.

mouth. Maxillipeds I, the maxillae, and the maxillules tossed and raked particles towards the mouth in a scissor-like manner.

Tenagomysis tasmaniae had their endopods spread, and the capture of particles often involved the scooping movements of maxillipeds II. The maxillipeds II stretched across the mouth chamber and extended anteriorly. These appendages mainly used their folded dactyli to scrape off particles. Processing of beads was also achieved by the fling and clap movements of the three lower podomeres of the endopods and the scissor-like raking motion of the mouthparts.

Beads trapped on the antennules, antennae, and antennal scales were brought to the mouth by grooming behaviour. Often done after grooming these appendages, the mandibular palps of *T. tasmaniae* touched the other mouthparts and the maxillipeds II. The cage formation appeared to accumulate a bolus of beads. Flanked on both sides by the first pair of maxillipeds, the tails of the young in the brood pouch also pushed trapped food particles to the mouth region.

Some particles gathered on the mouthparts were processed and ingested. Once captured and gathered about the mouth region, beads were sucked into the mouth region, and chewed by the mandible. Apparently due to size, the two largest bead categories were often rejected.

Bead Rejection

Bead rejection mechanisms were similar in the three mysid species. The majority of the beads were either drawn dorsally by the strong exopod currents. If the animal happened to have its endopods adpressed, the boundary layer effects in a streamlined individual did not allow capture of particles. After mandibular chewing and attempts at ingesting the beads, the reverse fling and clap of the three lower podomeres of the endopods, and the reverse scissor-like movements of the mouthparts rejected particles away from the mouth chamber along similar routes towards the ventral and posterior region. Tail flipping also removed trapped particles on the different appendages.

Ingestion of Beads

The number and size range of beads ingested varied among the three species of mysids (Table 3.1). *A. mixta australis* ingested mainly the smallest bead size, and some of size classes II and III. Beads, 10 to 65 μm in size, were ingested by *P. rufa*, while all size classes were ingested by *T. tasmaniae*. The three mysid species' ability to ingest bead size classes I to IV varied significantly except the last size class which was ingested only by *T. tasmaniae* (Table 3.2). Comparable numbers of beads were ingested by *P. rufa* and *A. mixta australis* (Table 3.3). Number and range of bead size classes ingested by *T. tasmaniae* differed significantly from the other two species (Table 3.3).

Proportions of bead sizes in control and experimental jars prior to feeding did not differ significantly (Student's two tailed t-test, df = 6, $p < 0.05$). The different sizes of beads available to the three mysid species varied in terms of relative proportion. This is shown by the average percentages of available and ingested beads in Figure 3.5. Numbers of the three smaller size classes of beads ingested by *P. rufa* were proportional to the number of available beads (Student's two tailed t-test, $p > 0.05$ for the three size classes of beads ingested). However, some fragments of bead type V were found in the stomachs of *P. rufa*. In contrast, *T. tasmaniae* ingested types I to III beads in proportion to availability, but type IV beads disproportionately (Student's two tailed t-test, $p < 0.01$ for both size classes). *T. tasmaniae* also showed a proportionate ingestion for the largest bead size(Student's two tailed t-test, $p > 0.05$). *A. mixta australis* disproportionately ingested the smallest bead size class (Student's two tailed t-test, $p < 0.001$), and types II and III beads proportionately.

Although very wide ranges of Ivlev's Electivity Index values were shown by the three mysid species, preference for certain size classes of beads was evident (Table 3.4). Positive values for the first two size classes of beads were shown by *P. rufa* indicating preference for these beads. Strong selection for the smallest bead size was shown by *A. mixta australis*. A weak selection for the two smaller bead size classes was shown by *T. tasmaniae*.

Table 3.1 Number of individuals in the three mysid species which ingested the different inert plastic beads over 20 min.

Paramesopodopsis rufa

no of beads	Bead Diameter (mean µm ± SD) 11.95 ± 2.45	20.73 ± 3.15	36.73 ± 5.50	64.98 ± 6.36	90.23 ± 9.78
1-2	3	17	12	7	
3-4	3	8	1		
5-6	1	6			
7-8	5	5			
9-10	2	1			
11-12	3	2			
13-14	3	2			
15-16	1	2			
17-18	5				
21-22	2				
23-24	1				
25-26	2				
29-30	1				
33-34	4				
35-36	2				
41-42	3	1			
50	1				
51	1				
63-64	2				
90	1				
99	1				

Tenagomysis tasmaniae

no. of beads	Bead Diameter (mean µm ± SD) 11.95 ± 2.45	20.73 ± 3.15	36.73 ± 5.50	64.98 ± 6.36	90.23 ± 9.78
1-2		17	18	6	4
3-4	8	10	5	7	1
5-6	6	10	3	1	
7-8	7	7		1	
9-10	11	6		2	
11-12	7	5	2		
13-14		3			
15-16	6	5	4		
17-18	4	3			
19-20	4	2	1		
21-22	1	1			
23-24	2	1	1		
25-26			2		
27-28	3				
29-30	3				
31-32		2			
35-36	1	1			
37-38		3	1		
41-42		1			
43-44		1			
45-46	2	1			
47-48	2				
49-50	1				
62-63	3	1			
71	1				
78	1				
81	1				
84	1				
87	1				
90	1				
97					
101	1				
124-125	3				
126	1				
143	1				
147	1				
185	1				
253	1				

Anisomysis mixta australis

no. of beads	Bead Diameter (mean µm ± SD) 11.95 ± 2.45	20.73 ± 3.15	36.73 ± 5.50	64.98 ± 6.36	90.23 ± 9.78
1-2	16	12	2		
3-4	17	4			
5-6	12	2			
7-8	8		1		
9-10	5	2	1		
11-12	2				
13-14	3				
15-16	3				
17-18	1	1			
21-22	1				
23-24	2				
25	1				
38	1				
41	1				
50	1				

Table 3.2 One-way analysis of variance (ANOVA) for the number of ingested beads of different sizes by the three mysid species.

Bead size (mean μm ± SD)	*F*	df	*p*
11.95 ± 2.45	7.061	2	< 0.010
20.72 ± 3.15	10.283	2	< 0.001
36.73 ± 5.50	7.448	2	< 0.010
64.98 ± 6.36	7.660	2	< 0.001
90.23 ± 9.78	2.221	2	> 0.100

Table 3.3 Tukey's Honestly Significant Difference test to compare average number of beads of different sizes ingested by the three mysid species. P =*Paramesopodopsis rufa*; T = *Tenagomysis tasmaniae*; A = *Anisomysis mixta australis*; subscript = bead size (mean μm ± SD) (I = 11.95 ± 2.45, II = 20.72 ± 3.15, III = 36.73 ± 5.50, IV = 64.98 ± 6.36, V = 90.23 ± 9.78).

	P_I	P_{II}	P_{III}	P_{IV}	P_V	T_I	T_{II}	T_{III}	T_{IV}	T_V	A_I	A_{II}	A_{III}	A_{IV}	A_V
P_I	1.000														
P_{II}		1.000													
P_{III}			1.000												
P_{IV}				1.000											
P_V					1.000										
T_I	0.012					1.000									
T_{II}		0.002					1.000								
T_{III}			0.002					1.000							
T_{IV}				0.003					1.000						
T_V					0.144					1.000					
A_I	0.674					0.005					1.000				
A_{II}		0.501					0.000					1.000			
A_{III}			0.958					0.028					1.000		
A_{IV}				0.925					0.007					1.000	
A_V					1.000					0.279					1.000

Table 3.4 Ivlev's Electivity Indices for the three mysid species feeding on inert plastic beads.

Paramesopodopsis rufa

Beads size (mean µm ± SD)	Range	Mean ± SD
11.95 ± 2.45	-0.12 - 0.94	0.20 ± 0.40
20.72 ± 3.15	-0.20 - 0.63	0.25 ± 0.25
36.73 ± 5.50	-1.00 - 0.80	-0.40 ± 0.59
64.98 ± 6.36	-1.00 - 0.60	-0.90 ± 0.14
90.23 ± 9.78	-1.00	-1.00

Tenagomysis tasmaniae

Beads size (mean µm ± SD)	Range	Mean ± SD
11.95 ± 2.45	-0.05 - 0.13	-0.01 ± 0.22
20.72 ± 3.15	-0.52 - 0.24	-0.01 ± 0.23
36.73 ± 5.50	-1.00 - 0.46	-0.10 ± 0.49
64.98 ± 6.36	-1.00 - 0.43	-0.60 ± 0.56
90.23 ± 9.78	-1.00 - 0.57	-0.80 ± 0.28

Anisomysis mixta australis

Beads size (mean µm ± SD)	Range	Mean ± SD
11.95 ± 2.45	-0.06 - 0.21	0.10 ± 0.09
20.72 ± 3.15	-1.00 - 0.25	-0.50 ± 0.15
36.73 ± 5.50	-1.00 - 0.40	-0.60 ± 0.60
64.98 ± 6.36	-1.00	-1.00
90.23 ± 9.78	-1.00	-1.00

Individual clearance rates in the three species are shown in Figure 3.6. *T. tasmaniae* individuals showed a wider range of clearance rates compared to the other two species. *T. tasmaniae* individual clearance rate ranged from 3 to 300 µL mysid^{-1} h^{-1}. *P. rufa* individuals showed a range from 1 to 120 µL mysid^{-1} h^{-1}. In contrast, *A. mixta australis* showed a range of 1 to 70 mL mysid^{-1} h^{-1}. Figure 3.7 shows a similar scatterplot for bead ingestion rates by the three mysid species. A wider range of ingestion rates from 12 beads mysid^{-1} h^{-1} to a maximum of 1076 beads mysid^{-1} h^{-1} was shown by *T. tasmaniae* . *P. rufa* ingestion rates ranged from 6 to 424 beads

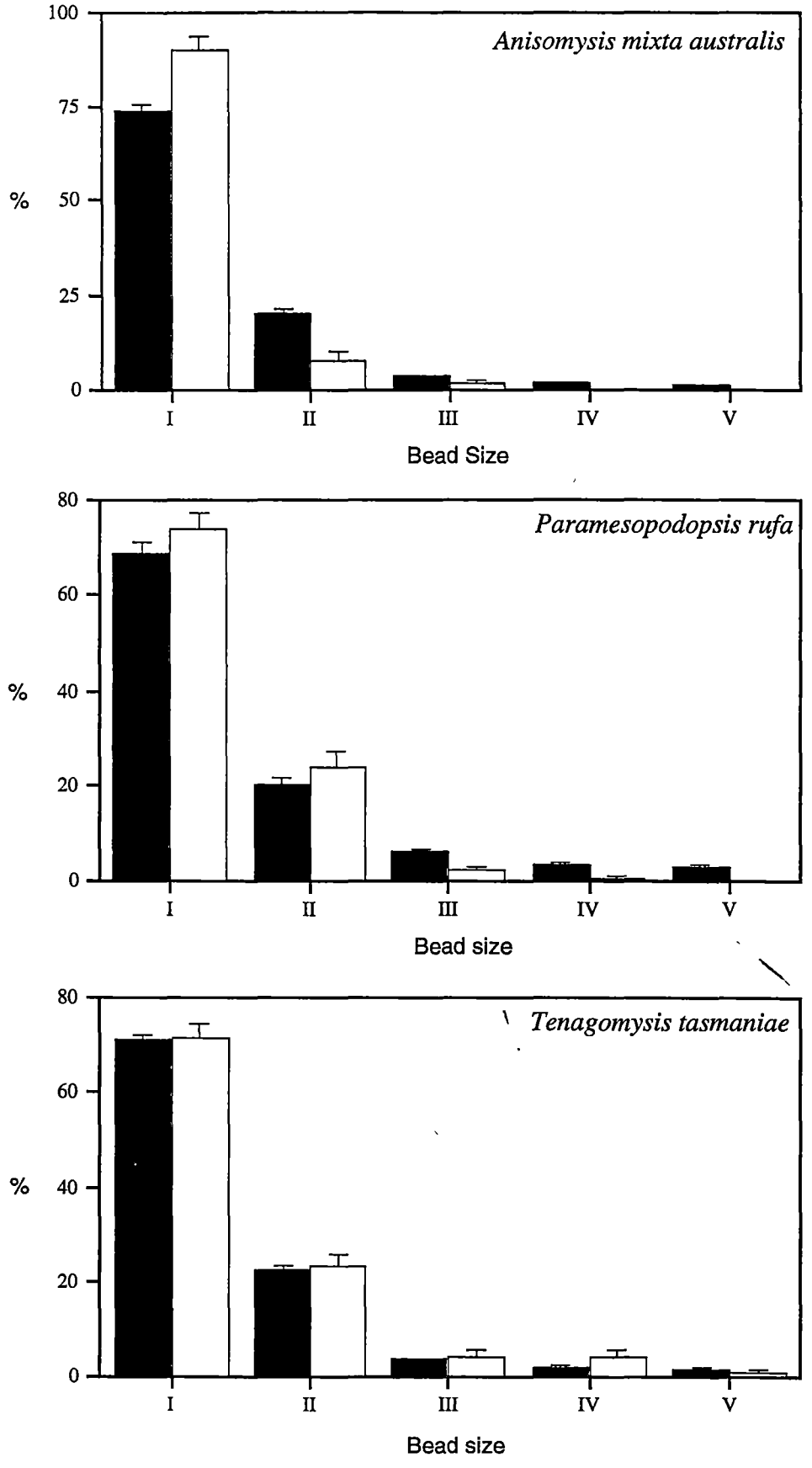


Figure 3.5 Average percent available (solid bars) and average percent ingested (open bars) beads from the feeding experiment with the three co-occurring mysid species. Error bars: SE.

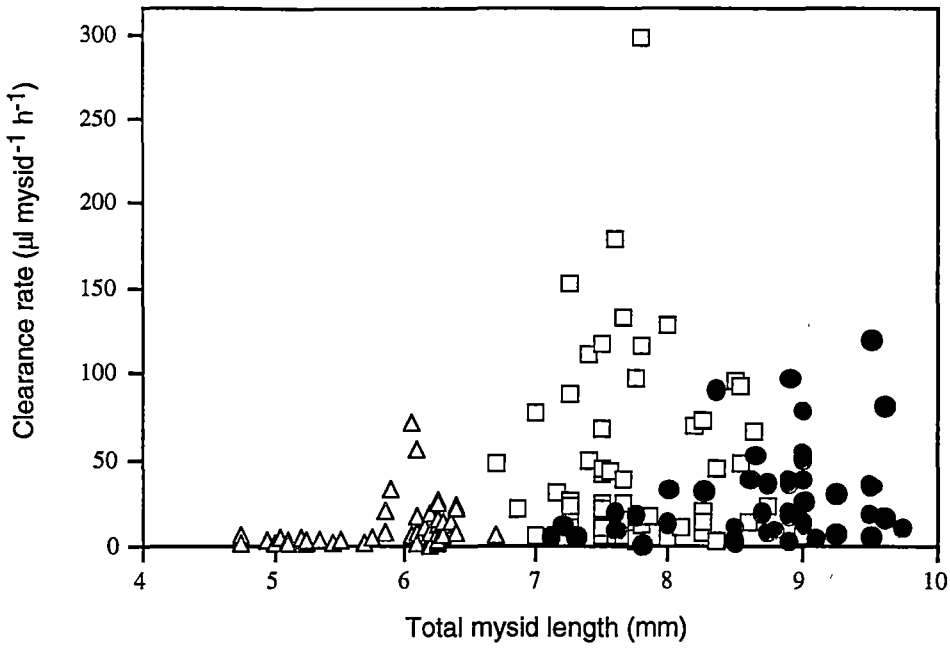


Figure 3.6 Volume of seawater cleared of inert beads by the three mysid species. Triangles - *Anisomysis mixta australis*, circles - *Paramesopodpsis rufa*, squares - *Tenagomysis tasmaniae*.

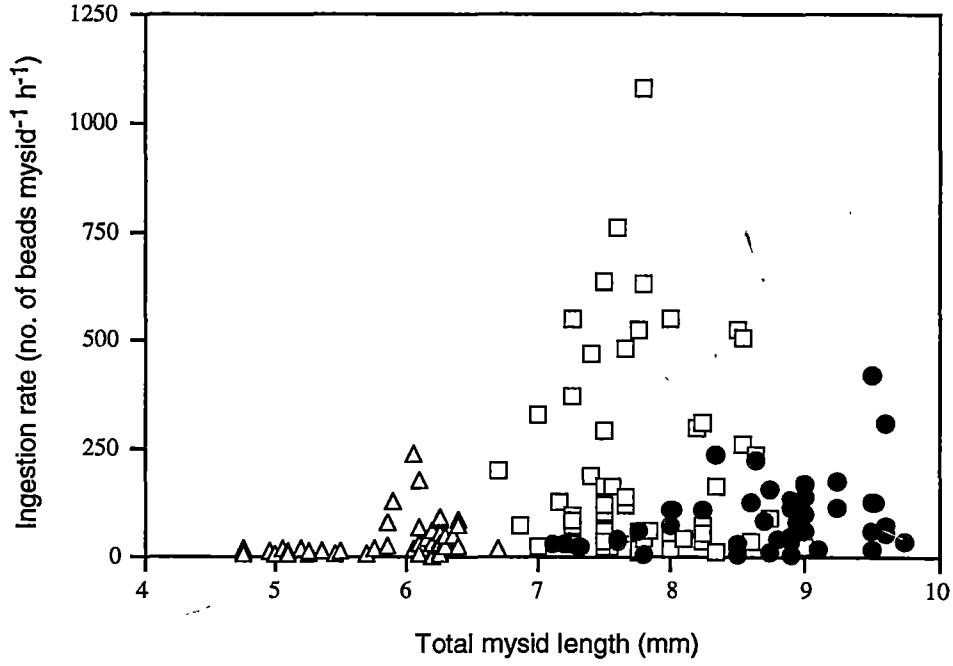


Figure 3.7 Ingestion rates of inert beads by the three mysid species. Triangles - *Anisomysis mixta australis*, circles - *Paramesopodpsis rufa*, squares - *Tenagomysis tasmaniae*.

mysid^{-1} h^{-1}. *A. mixta australis* showed a similar minimum of 6 beads mysid^{-1} h^{-1} to that of *P. rufa*, and a maximum of 236 beads mysid^{-1} h^{-1}.

Discussion

Feeding Mechanisms

In the three species, the rapid movement of the exopods was found to be metachronal (see Laverack *et al.* 1977; Hessler 1985; Bowers *et al.* 1990; Schabes and Hamner 1992) and revealed no axial currents. This movement involves the antero-posterior successive beating of the exopods each of which follow elliptical paths (Laverack *et al.* 1977). Cannon and Manton (1927) noted that the currents generated by the beatings not only propels mysids while swimming, but also produce a food stream and respiratory current. Schabes and Hamner (1992) reported that Cannon and Manton's (1927) exopod axial currents do not exist; rather these limbs operate as a metachronally beating unit. The vibrations in the endopods are derived from the rapid exopod movements in as much as the animal has biramous legs attached to the same basis (Hessler 1985).

A recent study of amphipods which are capable of occasional swimming showed that these animals swimming at intermediate Reynolds' number have a streamlined body shape (Boudrias 1991). Boudrias concluded that streamlining in swimming amphipods confers drag reducing advantages to the animal. Mysids, no doubt, take advantage of body shape streamlining while swimming.

Outstretching closely resembles that of a raptorial method of capturing large particles, *i.e.* grasping a large prey, where the gape formed by the vertically stretched endopod would be dependent on the size of the prey. Apparently, chemical or tactile stimuli may have induced this behaviour since it is shown only upon approach and contact of the food particles. Contact or far-field chemoreception may trigger this behaviour; indeed, a wide variety of chemo-mechano-sensory setae are present on mysid thoracic endopods (Crouau 1982, 1989). Proteins and free amino acids from

the mysid homogenate and the fish suspension were probably detected by chemoreceptors which gave the animal cues of an animal prey (see Zimmer-Faust 1987). Alternatively, visual cues provided by the dense cloud of fish particles may also be important in eliciting this behaviour. The ventral outstretching of endopods exposed the setae projecting from the medial surface of the podomeres. Perhaps, like the endopods of euphausiids, these setae all project towards the mouth region when their bearers are adpressed to the ventral thoracic region (Hamner 1988).

Usually following after outstretching, cage formation has been observed in the chemoreception study (chapter 2), and this limb posture was adjudged as a prey restraining posture. Indeed, in the predatory feeding behaviour (chapter 4) primary and secondary cages were used by *P. rufa* and *A. mixta australis*, and mainly the primary by *T. tasmaniae*.

The endopods played a major role in all *P. rufa* grooming behaviour as the same grasping movements were performed on the above appendages. Among natant decapod shrimps grooming is done by the chelipeds and posterior periopods which bear patches of serrate setae (Bauer 1989). Grasping and subsequent grooming of these appendages by the endopods was similar to the stereotyped outstretching behaviour. Strickler (1984) noted that in calanoid copepods, the orientation and positioning of the appendages involved during grooming and food capture do not show marked differences, and that grooming is a pre-adaptation for predation. It has often been suggested that grooming behaviour is closely allied with fine particle feeding in a variety of crustaceans (Strickler 1984; Bauer 1989; Holmquist 1989). McGrouther (1983) reported setal transfer type of feeding in amphipods following grooming behaviour.

Regular grooming is required to keep the antennae and associated structures free from fouling agents such as epizoonts, microbes and potential parasites (Bauer 1989). Grooming the antennae and the antennules ensures that the chemosensory setae, particularly the aesthetascs, function optimally. It is worth mentioning that the flicking forwards and the lowering of the antennules ventrally in *P. rufa* is a behaviour also displayed in natant and reptant decapod shrimps (Bauer 1989).

Following the suction mechanism generated by "outstretching" and "feeding bout", capture of fine food particles may be achieved by the impaction method (Rubenstein and Koehl 1977). This method involves the coalescence of boundary layers of both the fine particle and either the setae and/or the podomeres of the endopod. Thus, utilization of these attached fine food particles can only be achieved by cleaning movements (*sensu* Attramadal 1981). However, this particle capture mechanisms could become unoperational when the endopods are adpressed because of the apparent thick boundary layer covering these appendages (see Koehl and Strickler 1981; Hamner 1988). By viewing *P. rufa* from different angles it was apparent that fine particles did not enter at all at the front, sides and back of the adpressed endopods. In addition, the mysid homogenate approaching the adpressed endopods was not able to flow between these limbs.

Cessation of the rapid exopod movement brought all particles in the vicinity of the adpressed endopod limbs to a halt. Strickler (1984) presented the "breakfast table experiment" which explained the behaviour of a particle in the vicinity of crustacean limbs wrapped with thick boundary layers. Because both the limb and the particle operate in a highly viscous environment, the particle should move along with the direction of a limb. If a pair of limbs facing each other performs the "clapping" motion, the particles near the tip of the limbs should be carried away with the direction of the limbs. On the other hand, if the same appendages perform the "flinging" motion the same particle will be sucked in between the two flinging limbs. In the present study, a 10 μm diam. particle very near the lower three podomeres was observed moving along with the direction of the limbs, thus demonstrating the outcomes of the "breakfast table experiment."

These observations on the feeding responses of the three mysid species to various food suspensions confirm the findings of Depdolla (1923) and Schabes and Hamner (1992) that food particles are captured from the ventral cephalothoracic region of the animal. These observations further support Attramadal's (1981) findings that the ventral feeding currents described by Depdolla (1923) and Cannon and Manton (1927) are experimental artefacts. The boundary layer theory and

streamlining of body shape explain the absence of ventral filter feeding currents. Furthermore, this study, agrees with the conclusions of Attramadal (1981) and Schabes and Hamner (1992), calling for the abandonment of the exopod "axial streams" of Cannon and Manton (1927). On the other hand, "cleaning movements" (*sensu* Attramadal 1981) and/or grooming behaviour of different body parts to some extent contribute to the collection and subsequent ingestion of fine food particles in mysids. The behaviour of feeding appendages is apparently similar in *Paramesopodopsis rufa* and *Anisomysis mixta australis*. That of *Tenagomysis tasmaniae* is distinct which may be attributed to the fact that this third species is more of a substrate specialist in contrast to the other two species which are pelagic (Wittmann 1977).

Particle Size Selection

The capture of inert beads by the three mysid species was achieved by grooming, scooping and raking movements of feeding appendages, while rejection was by reverse movements of these appendages. This stereotyped concerted movement of legs resembles that used for grasping large objects and suggests that the mysid may mistake clouds of particles for one big particle. It is interesting to note that tails of pouch young also helped push particles to the mouth region of gravid females. A strong tail flip quickly removed particles, suggesting that the mysid may perform a rapid escape response from a patch of indigestible, inert or lower value food. Lowering of mandibular palps may have a role in manipulating current flow in the mouth region directing particles to the mouthparts. The maxilliped II in *T. tasmaniae* played a major role in bead processing. The effect of the boundary layer may be evident from the fact that beads decreased in speed near the limb surface and became entrapped on these appendages.

The present study provides evidence for the potential range of particle sizes that the three mysid species could ingest. Feeding on beads has been reported in other aquatic suspension feeding crustaceans. Miller (1984) noted that the amphipod

Corophium sp. can ingest up to 7200 beads individual^{-1} h^{-1} when suspension feeding on 9 μm diameter beads at comparable densities offered to the three mysid species. Calanoid copepod nauplii have been reported to ingest 1.2 μm size plastic beads at a maximum of 820 beads individual^{-1} h^{-1} (P-Zankai 1991). Copepodite stages of *Acartia tonsa* can clear > 40 μL individual^{-1} h^{-1} at 1000 to 2000 beads mL^{-1} suspension of 45 mm size particles (Hansen *et al.* 1991).

Earlier studies have noted that mysids use passive filtration mechanisms to collect fine food particles (Depdolla 1923; Cannon and Manton 1927). However, as already mentioned above, Attramadal (1981) reported the absence of a ventral filter-feeding current as had been expected from the properties of particles and fluids at the size scale of mysid mouthparts, and other feeding appendages. When offered fine food particles, the endopods of *P. rufa* and *A. mixta australis* remained adpressed to the underside of their thorax, and because of the thick boundary layer enveloping these appendages (see Koehl and Strickler 1981), it is unlikely that fine particles could be captured through these folded limbs. However, regular lowering of endopods and mouthparts grooming behaviour may be invoked as a probable method in the collection of inert plastic beads by the three mysid species.

On the other hand, because *T. tasmaniae* displays both cleaning mechanisms and a characteristic bolus formation of collected particles in its mouth chamber, it may be capable of relatively higher values of bead ingestion compared to the other two species. Grooming behaviour has been associated with anti-fouling, but its role in mysid feeding remains to be established (Acosta and Poirrier 1992). How these small particles are trapped on the surfaces of thoracic limbs may be explained by various alternative mechanisms by which fine particles are captured (Rubenstein and Koehl 1977). Particles that managed to enter the mouth region may be processed by the mouthparts and their complex setal systems. Each of these individual setae usually bears setules on its basal parts which may play a major role in capturing smaller particles, while the distal part may be involved in the raptorial capturing process of larger particles (Gauld 1966 cited in Tiselius and Jonsson 1990).

Occasional or periodic movements of mouthparts, particularly the mandibles, can perhaps explain the fact that only a small size range of beads were preferentially ingested and were most abundant in the stomachs of the three mysids. In addition, particle ingestion may solely depend on the diameter of the mouth orifice. The elasticity or distensibility of the oesophagus during peristaltic transport of ingested particles may also determine the upper limit of the size of particles ingested by the animal. Therefore, there exists an apparent post-capture size selection of particles by mysids brought about by purely mechanistic or morphological reasons. Vanderploeg (1990) noted that smaller sizes of inert particles are more passively ingested. Concentration of particles in the medium also determines ingestion of inert particles. In the present experiment, the concentration of particles introduced was high enough to ensure ingestion despite the fact that these particles possess no nutritional qualities.

Once captured, beads being non-food particles are subject to post-capture active rejection. Inert plastic beads have been reported to cause reduced feeding rates in many suspension feeding calanoid copepods by active avoidance behaviour and post-capture rejection (Donaghay and Small 1979; Vanderploeg 1990; Hansen *et al.* 1991). Particle rejection may be under the influence of the animals' built-in "frustration" factor, which readily causes them to give up any further attempts at ingesting if particles which after being "tasted" turn out to be too big to be ingested or too hard to be broken by the cracking structures of the mandibles (Strickler 1984). The "frustration" factor can be linked with increased time spent in handling and positioning of sub-optimally sized particles in the mouth region. Micro-cinematographic observation of *Eucalanus* revealed that many attempts were made by the copepod to ingest glass particles but all of them were unsuccessful and none were ingested at all (Strickler 1984). The ability to discriminate food from non-food microcapsules has also been shown in many planktonic calanoid copepods (Poulet and Marsot 1978; Demott 1989; Vanderploeg 1990).

Despite the slow revolution of the jars during the experiment, the larger beads, in particular the types IV and V beads size classes, would settle on the bottom

of the jar. This may further explain the relatively high ingestion rates of beads by *T. tasmaniae* which displays a characteristic behaviour of resting on or swimming very near the bottom of the experimental chamber. In this way, gross behaviour of a mysid species could exert some influence on feeding performance, and particle capture in mysids might depend on feeding behavioural repertoires which vary from species to species.

Although the present feeding study is inherently artificial because of the use of inert beads, some insights into the feeding behaviour by the three mysid species can be derived. As has been commonly noted in studies on other suspension feeding organisms, the use of plastic or glass spheres or beads removes effects of quality such as taste and geometry or shape which may greatly influence feeding behaviour of organisms (Miller 1984). Size of suspension feeding arthropods is an important factor that determines the range of particle size ingested (Burns 1968; Wilson 1973; Fenchel *et al.* 1975; Schrøder 1987). The size of the different mysid species also influences the particle size ingested as shown by positive selection for the smallest size of beads in *A. mixta australis.* The two larger species showed some degree of overlap in the sizes of particles ingested, but behavioural features may separate these species.

Although showing a strong overlap of the sizes of beads ingested, the present study demonstrates the capacity of the three mysid species to select different sized inert beads. Mysid size and feeding behavioural differences play a dominant role in the capability to collect and ingest the various sizes of inert plastic beads. The very low clearance and ingestion rates of these particles may be a reflection of high frequency of rejection of inert non-nutritive particles. Nevertheless, the present study demonstrates a probable mechanism by which the three co-occurring mysid species partition their fine particulate food and that is by particle size.

CHAPTER 4

PREDATORY FEEDING BEHAVIOUR

Introduction

The predatory feeding behaviour in many zooplanktonic species has been recognized as a complex system, which requires more detailed study to elucidate its intricacies (Steele and Frost 1977; Kerfoot 1980; Price 1988; Ohman 1988; Gliwicz and Pijanowska 1989). These reviews also noted that the success of predation is influenced primarily by the size and/or stages of both predators and prey (Gliwicz and Pijanowska 1989). In predator-prey interaction, predators are generally larger than their prey (Mullin 1963). However, various morphological (body pigmentation, Zaret 1972; shape, Swift & Fedorenko 1975), physiological (palatability, Kerfoot 1982), and behavioural (motion, Zaret 1980; escape reactions, Drenner *et al.* 1978) features explain the vulnerability to predation of prey (Ohman 1988; Gliwicz & Pijanowska 1989).

The predatory nature of mysids in many freshwater and estuarine environments is well documented (*e.g.* Mauchline 1980; Siegfried & Kopache 1980; Murtaugh 1981 a,b; Folt *et al.* 1982; Fulton 1982; Wooldridge & Bailey 1982; Chigbu and Sibley 1994). These studies demonstrate how efficient many mysid species are as invertebrate planktivores. For example, *Mysis relicta* (Cooper & Goldman 1980; Ramcharan *et al.* 1985; Lasenby *et al.* 1986; Ramcharan & Sprules 1986; Lehman *et al.* 1990), *Neomysis mercedis* (Murtaugh 1981 a,b; Chigbu and Sibley 1994), *N. intermedia* (Hanazato 1990), and *N. integer* (Bremer & Vijverberg 1982) can significantly reduce numbers of zooplanktonic cladoceran populations. Benthic harpacticoid copepods (Mauchline 1971c, Johnston and Lasenby 1982), calanoid copepods (Siegfried and Kopache 1980; Wooldridge and Bailey 1982; Fulton 1982; Mauchline 1970; Hansson *et al.* 1990 and the nauplii of *Artemia* sp. (Clutter and Theilacker 1971; Reitsema and Neff 1980; Vos *et al.* 1984; Mullin and Roman 1986;

Ward 1987) are preyed upon by mysids.

Despite the vast information on the predatory feeding habits by these mysid species few studies on the functional response of mysids to prey availability have been undertaken (*e.g.* Murtaugh 1980a,b; Siegfried and Kopache 1980; Fulton 1982, 1983; Folt 1985; Wooldridge and Webb 1988). The lack of detailed knowledge on aspects of mysid predatory behaviour is also apparent. Bowers & Vanderploeg (1982) noted that knowledge of predator-prey contact frequency, prey swimming speeds, prey escape behaviour, capture success, and prey handling times is needed to further the understanding of mysid feeding behaviour. In a recent review by Price (1988), the importance of Holling's (1959a,b) models of predation in zooplankton predatory behaviour studies has been emphasised. Predation, based on this framework, can be broken down into a cycle of sequential component events comprising encounter, attack/pursuit, capture, and ingestion (Gerritsen & Strickler 1977). A detailed picture of predator-prey interaction can be obtained because each event can be analysed and quantified separately (O'Brien 1979; Landry & Fagerness 1988).

Different mysid species vary in size and overall predatory feeding behaviour which are also highly likely to influence rates of predation on the various prey types. These differences in predatory feeding behaviour in co-occurring species may act as a mechanism of resource partitioning (Paffenhøfer 1988; Vanderploeg 1990). In the present study, the handling (capture and ingestion) component of predation in the three mysid is analyzed in detail. In particular, (1) limb postures associated with prey capture are described, (2) prey capture, ingestion, and handling times, and the velocities of the capturing limbs are quantitatively estimated, and (3) results from (1) and (2) in the different stages of the three species are compared. Also, the functional responses of three co-occurring mysid species are examined using different types of prey.

Materials and Methods

Field collection and laboratory maintenance of the three species of mysids used

in both feeding mechanisms and functional response experiments are described in chapter 2.

Predatory Feeding Mechanisms

Experimental Prey Animal

Adult *Daphniopsis australis* individuals were collected from a fish farm at Triabunna, east Tasmania, and were allowed to proliferate in 50-L tubs containing 5 µm Millipore filtered seawater diluted to 20 ‰ with treated effluent from a sewage works, and at ambient temperature (12-14 °C). Under these conditions, juveniles became abundant in the tanks a week later. *D. australis* individuals were allowed to acclimatise for 15 min to full strength (34-35 ‰) seawater prior to use in the experiments. Mysid field collection and maintenance in the laboratory are described in chapter 2. The three mysid species do not normally encounter *D. australis*; I selected this prey because in the laboratory, (1) it is easily cultured, and (2) it is readily captured and eaten by mysids.

Mysid Tethering and Filming Set-up

Observations of behaviour were done on tethered individuals, and the experimental set-up and tethering procedure are also described in detail in chapter 2.

Observations (10 min for each mysid predation category) were recorded on S-VHS casette tapes using a Panasonic (CCTV, Model WV-BL600/B) camera and a Panasonic (Model NV-FS100HQ) VCR. Soon after filming, the mysids were detached from their tethers and preserved in 5% (v/v) buffered formalin in seawater. Total length (measured from the tip of the rostrum to the tip of the telson) was recorded for each mysid. *D. australis* total lengths (anterior tip of the head to posterior tip of carapace) were measured from the TV screen, by reference to a calibration scale in the picture, during film analysis which was done by

playing back the videotape at appropriate film speeds. For illustrations of prey capture, a frame grabber was used to capture single video frames from the videotape. Images were enhanced in a Power Macintosh computer, laser-printed, and assembled into a collage of pictures.

Analysis of Prey Capturing Limb Postures and Velocities, and Prey Capture, Ingestion, and Handling Times

Eight mysid predation categories, each of which comprised a combination of a predator stage and sex and a prey instar, were observed (Table 4.1). Five replicate

Table 4.1 Mysid predation categories used in the video recording. Sufficient numbers of all categories were only available for *P. rufa*.

Mysid stages/sex	*Daphniopsis australis* instar*	Abbreviation
Mature Female	Juvenile	FJ
Mature Female	Adult	FA
Mature Male	Juvenile	MJ
Mature Male	Adult	MA
Immature Female	Juvenile	IFJ
Immature Female	Adult	IFA
Immature Male	Juvenile	IMJ
Immature Male	Adult	IMA

*size of juveniles: mean ± SD = 0.85 ± 0.14 mm; range = 0.68 - 1.25 mm; n = 20
size of adults: mean ± SD = 1.90 ± 0.15 mm; range = 1.66 - 2.03 mm; n = 20

observations were made for each predation category. The behaviour of thoracic appendages involved in live prey capture, handling and ingestion was examined at different angles, and all observations commenced after the prey was introduced near the anterior region of the tethered mysid using a wide bore pipette. This procedure ensured very rapid prey capture. The distance at which a limb was displaced relative to its streamlined position was measured from the TV screen. These distance measurements were multiplied by a constant (the true outer diameter or O.D. of the

tether divided by its O.D.) to get the actual distance in mm. Limb extension duration was obtained by counting the number of 19 ms frames (duration of a frame at normal speed) it took for the limbs to stretch fully. The velocity of the displaced limbs was calculated by dividing the distance values by the duration measurements. Prey handling time was defined as the period comprising prey capture and start of ingestion. To determine prey capture time, the number of frames that followed after the prey came in contact with the endopods until the first bite by the mandibles was counted. Prey ingestion time was recorded as the duration from the subsequent mandibular bites until the entire consumption of the prey.

Functional Response Experiments

Experimental Prey Animals

Juvenile *Daphniopsis australis* were obtained from the cultures described above.

Mature cysts of *Artemia* sp. (Artemia Revolution, New Technology, Kent, England) were hatched in the laboratory at 24 °C water temperature and 40 ‰ salinity. Two day old metanauplii were used in the predation experiments.

Adult *Gladioferens pectinatus* were collected from six locations in the Derwent Estuary at a depth of either 1 m or 20 m using a 300 µm mesh conical net. In the laboratory, these animals were kept in 50-L plastic tubs containing seawater from the sampling area. At the time of collection, a large bloom of *Coscinodiscus wailesii* occurred. Buckets of these diatoms were collected and placed into the copepod tubs to serve as food. During the entire period of the experiment, the tubs with food and copepods were gently aerated, and kept at ambient temperature (15 °C), and at constant ambient salinity of 34 ‰.

All feeding experiments were performed simultaneously with each of the three species held separately. The predation chamber was made of a 2-L glass jar, wrapped entirely with black electrical tape to block any light, and filled to the brim with 5 µm Millipore-filtered seawater. This chamber was covered with a tightly fitting black lid, placed onto a "plankton roller" and allowed to rotate at 0.83 ± 0.02 SD rpm. The

Millipore-filtered seawater. This chamber was covered with a tightly fitting black lid, placed onto a "plankton roller" and allowed to rotate at 0.83 ± 0.02 SD rpm. The design of the chamber ensured the absence of refuges such as the surface film and prevented prey congregating due to uneven light distribution. The prey were individually pipetted into the chamber to give densities of 5, 10, 15, 20 L^{-1} for *D. australis* and *G. pectinatus*. Treatment densities of *Artemia* metanauplii were 7.5, 15, 30, and 45 L^{-1}. All of these prey densities were replicated four times. Feeding time which lasted for 2 h started when four unstarved adult mysids was introduced into the chamber. At the end of the predation period, the contents of the chamber were emptied into plastic buckets. Predator and prey were removed and killed by placing them in vials containing 5% (v/v) buffered formalin in seawater. From these preserved samples, predator total lengths and the number of remaining prey were determined. Prey total lengths were measured from the control jar individuals. No prey mortality was observed in the control jars, thus any missing prey from the experimental predation chambers were recorded as captures. Since the three species of mysids consume their zooplanktonic prey in its entirety, ingestion/predation rates were expressed as number of prey $mysid^{-1}$ $hour^{-1}$. Stomachs were dissected out to verify fullness and confirm that missing prey could be attributed only to ingestion.

Statistical Analysis

Limb velocities, prey capture, ingestion, and handling times recorded from the three species were analysed separately using a means model two-way ANOVA involving mysid predation categories with missing cells and species as the two independent factors. ANOVAs were followed by Tukey's Honestly Significant Difference test to determine which means were significantly different.

The non-parametric Kruskal-Wallis single factor analysis of variance (ANOVA) was also computed to test the null hypothesis that predation (=ingestion) rates between prey densities (treatments) were equal, while treatment means were compared using the non-parametric Q test statistic for multiple comparison for unequal

number of data with tied ranks (Zar 1984). The functional response curves of the three mysid species were described from the relationship between ingestion rate and prey density. Curve fitting was performed using linear regression with replication, and slopes were compared using analysis of covariance followed by a Tukey test to determine significant differences between slopes (Zar 1984).

All statistical analysis was conducted using the computer program SYSTAT for Macintosh computers (Wilkinson 1992).

Results

Microvideographic Observation of Predatory Feeding Behaviour

Table 4.2 shows that similar sizes of individuals of each mysid species (CV < 5%) were used for video recording.

Table 4.2 Mysid sizes used in the video recording.

Mysid species	Stage/Sex	Size (mean ± SD) in mm [range in mm]	n
Anisomysis mixta australis	Mature Female	6.18 ± 0.19 [5.70 - 6.40]	13
Paramesopodopsis rufa	Mature Female	9.76 ± 0.38 [9.25 - 10.30]	10
	Mature Male	9.36 ± 0.28 [9.10 - 9.60]	10
	Immature Female	7.34 ± 0.59 [6.80 - 8.15]	10
	Immature Male	7.47 ± 0.61 [6.70 - 8.40]	10
Tenagomysis tasmaniae	Mature Female	7.80 ± 0.85 [7.10 - 8.75]	6
	Mature Male	7.88 ± 0.80 [7.05 - 8.75]	7

Behaviour of Limbs During Prey Capture, Handling and Ingestion

Paramesopodopsis rufa

Prey Capture and Handling

The lateral view of the animal with endopods tightly adpressed on the underside of the thorax, and exopods in their rapid metachronal movement exhibited a streamlined body shape (Figs. 4.1a,j; 4.2a; 4.3a; 4.5a). The approach of prey initiated a slight lowering of the endopods, with the antennules and antennae brought to a perpendicular position in *P. rufa*. *D. australis* was motionless (akinetic) when it had just been released from the pipette and brought close to the endopods of *P. rufa* (Fig. 4.1a, 4.5a-d). However, upon outstretching of the second to the eighth pairs of endopods (E2 to E8) the prey showed a rheotactic response by a rapid and sudden flap of its antennae, bringing the body to a horizontal position exposing the dorsal surface of the carapace (Figs. 4.1d, 4.5e). If the prey was within the reach of the endopods, a successful capture followed, otherwise the prey escaped by swimming rapidly away from the tethered mysid.

Prior to prey capture, *P. rufa* showed an "outstretching" of endopods (Figs. 4.1c-e, 4.2b-e, 4.3b-e, 4.5d-f). This stereotyped endopod posture is characterised by the sudden ventral outsplaying of E2 to E8 followed by a series of rapid and sustained movements of these appendages. Observation of these endopod movements in slow motion reveals the basic crustacean "fling and clap" (*sensu* Weis-Fogh cited in Strickler 1984; cf Fig. 3.4) limb movements. Limb outstretching was elicited by the approaching prey, and the endopods remained stretched while vigorously flinging and clapping for as long as the prey was close to these limbs. Outstretching appeared to suck the prey towards the mouth region. During this behaviour, E2 to E8 varied in angles (10 to 120° range) relative to the ventral region of the thorax (Figs. 4.1e, 4.2c, 4.3c, 4.5e). Capture of prey by this limb posture was done occasionally antero-ventrally (front) to the animal, but more often, capture occurred when prey was ventral to the endopods. Endopods 2 and 3 often were involved in the successful prey capture (Fig. 4.1f,

4.5f). A primary "cage" is formed with E2 cradling the prey posteriorly, E1 and the other mouthparts tightly securing the prey on both sides, the mandibular palps forming an anterior cover (cf Fig. 3.2). During capture of juvenile *D. australis*, E2 and E3 reached out, and the moment the prey touched the medial surfaces of the lower three podomeres, these segments clapped medially embracing the prey. Then very rapidly (0.67 s ± 0.23 SE) the ischio-meral joints of E2 to E8 folded bringing the prey to the mouth region where it was securely gripped by endopods 1 and 2. Although different from the manner E2 and E3 capture prey, E4 - E8 were also used when capturing prey from the more posterior part of the thorax. Upon contact, these limbs merely flicked the prey towards E2 and E3. Capture of adult *D. australis* which lasted 1.49 s ± 0.24 SE, involved similar outstretching limb postures and then grasping by the endopods 2 and 3 (Figs. 4.2, 4.3). E4 to E8 stretched more posteriorly and were not involved in the prey capture. However, these limbs, because of the prey's large size, assisted the first two pairs of endopods in restraining it (Figs. 4.2h-j, 4.3g-j). Capture of both large and small prey involved the mandibular palps being lowered touching the dactyls and covering the anterior aspect of the prey grasping limbs. From this stage on until the prey was entirely ingested, E3 to E8 assumed the secondary "cage" formation covering the prey already contained in the primary "cage" (Figs. 4.1g,h). Joining the mouthparts, endopods 1 pushed the prey towards the mandibular blade. Prior to the first mandibular bite, the prey often struggled to free itself from the clasps of the endopods 1 and the embrace of the posterior endopods. However, a coordinated series of movements of the lower three podomeres of the endopods kept the prey in position with its longitudinal axis parallel to the body length of the mysid, and its dorsal surface in contact with the food groove.

Prey Ingestion

Soon after the prey was pushed in between the mandibular blades the first bite by the mandibles ensued. If the prey managed to struggle itself towards the

Figure 4.1 A series of video tape frames showing the capture and ingestion of a juvenile *Daphniopsis australis* by a mature female *Paramesopodopsis rufa*. Scale bar (frame a) is 0.6 mm long. The number in each frame is elapsed time in s. Arrow heads in frames f and g point the prey.

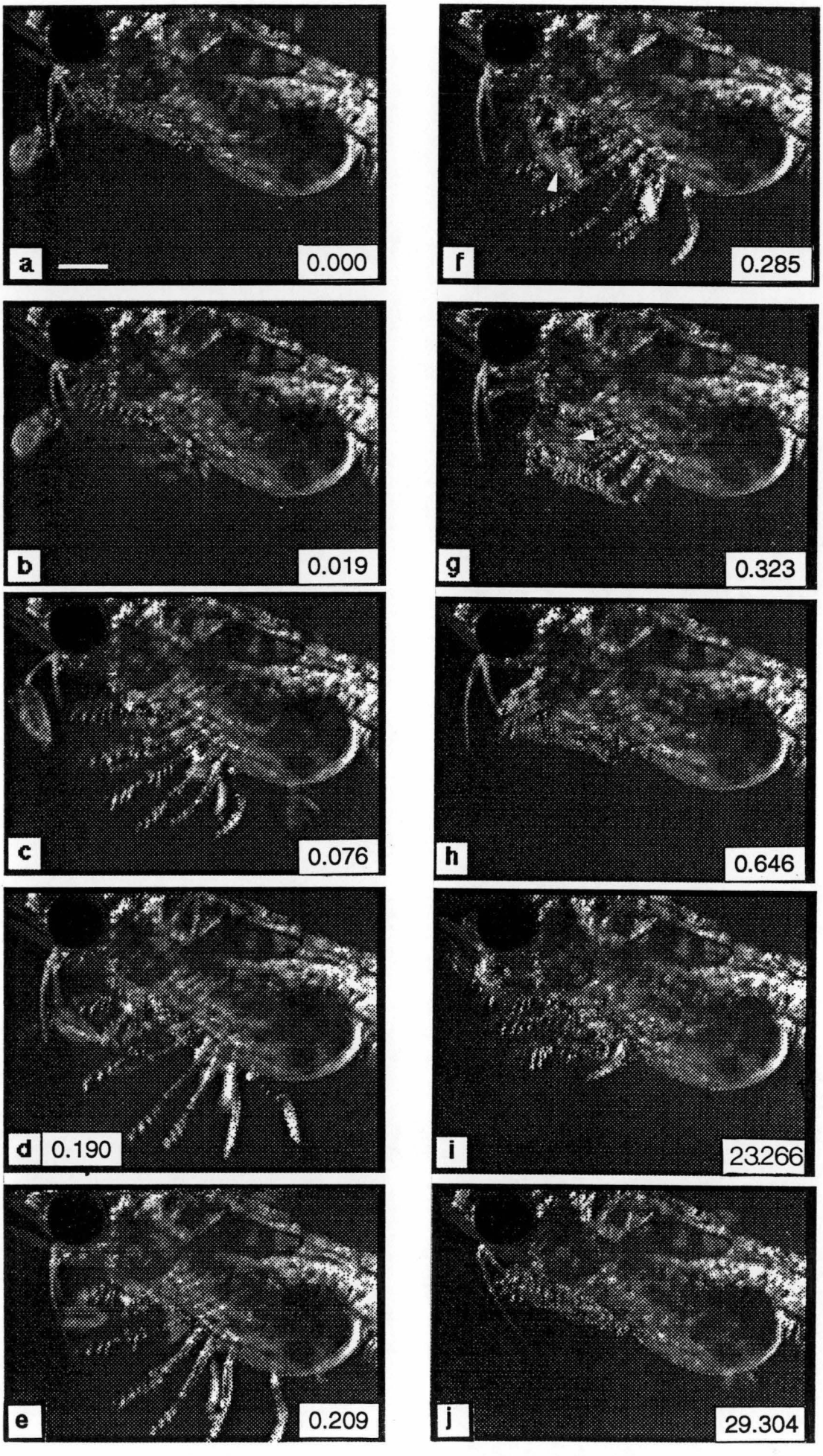
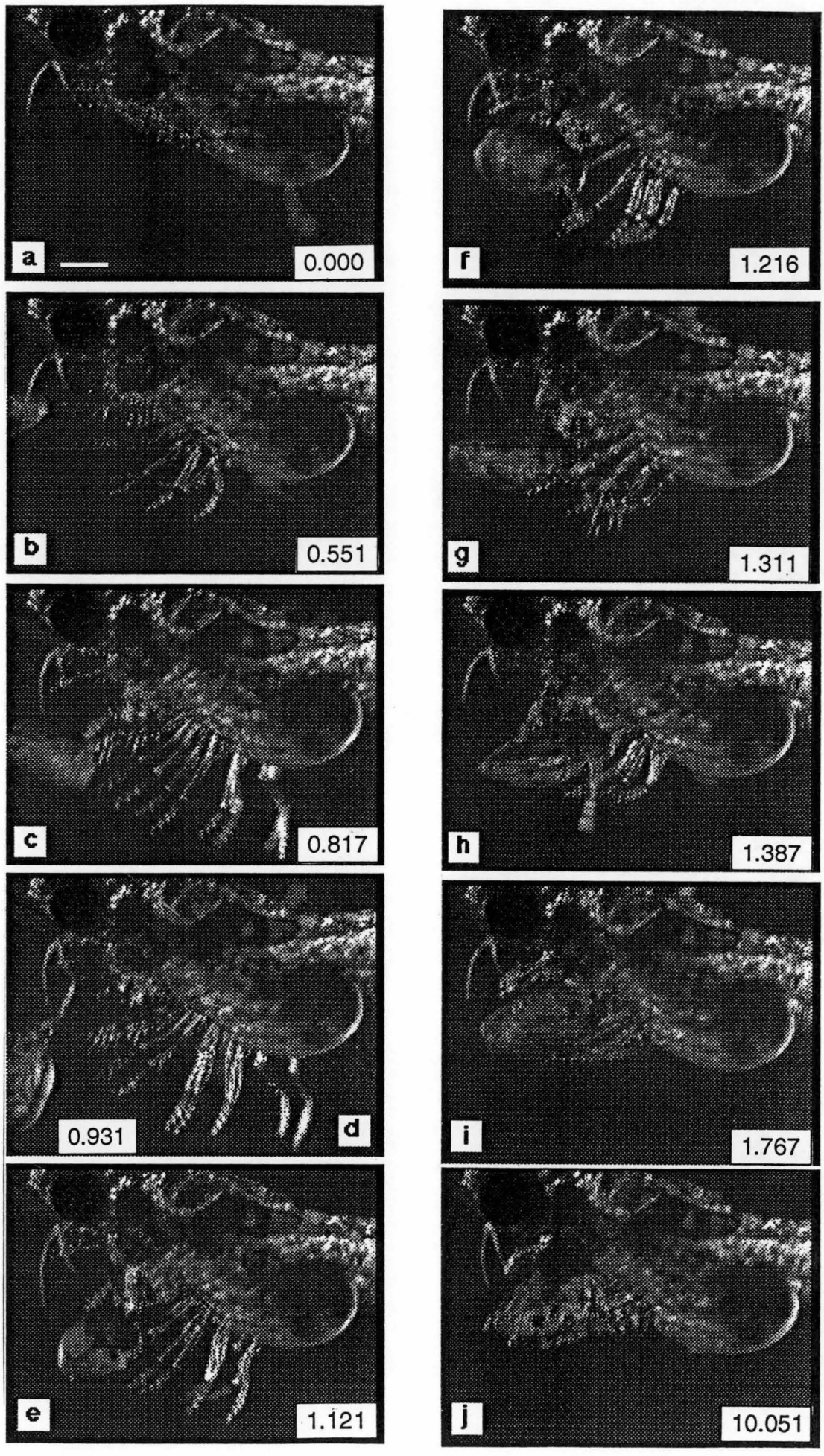

a
0.000
f
0.285
b
0.019
g
0.323
c
0.076
h
0.646
d
0.190
i
23266
e
0.209
j
29.304

Figure 4.2 A series of video tape frames showing the capture and ingestion of an adult *Daphniopsis australis* by a mature female *Paramesopodopsis rufa*. Scale bar (frame a) is 0.8 mm long. The number in each frame is elapsed time in s.


a
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f
1.216
b
0.551
g
1.311
c
0.817
h
1.387
0.931
d
i
1.767
e
1.121
j
10.051

Figure 4.3 A series of video tape frames showing the capture and ingestion of an adult *Daphniopsis australis* by a mature male *Paramesopodopsis rufa*. Scale bar (frame a) is 0.8 mm long. The number in each frame is elapsed time in s.

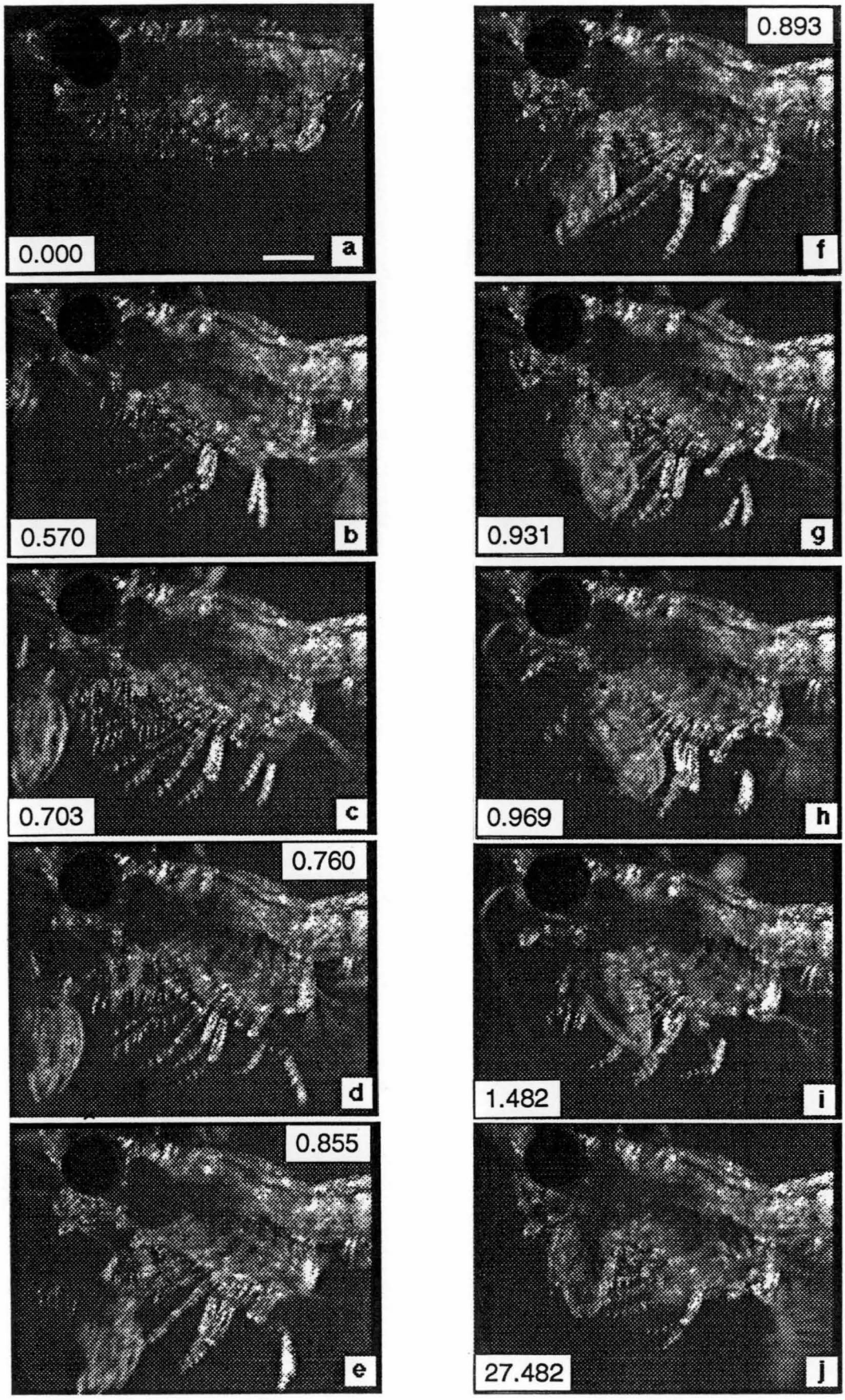

0.000
a
0.570
b
0.703
c
0.760
d
0.855
e
0.893
f
0.931
g
0.969
h
1.482
i
27.482
j

Figure 4.4 A series of video tape frames showing the rejection of an ephippium from an adult *Daphniopsis australis* by a mature male *Paramesopodopsis rufa*. Scale bar (frame a) is 0.8 mm long. The number in each frame is elapsed time in s. Arrow heads in frames a-f point the ephippium.

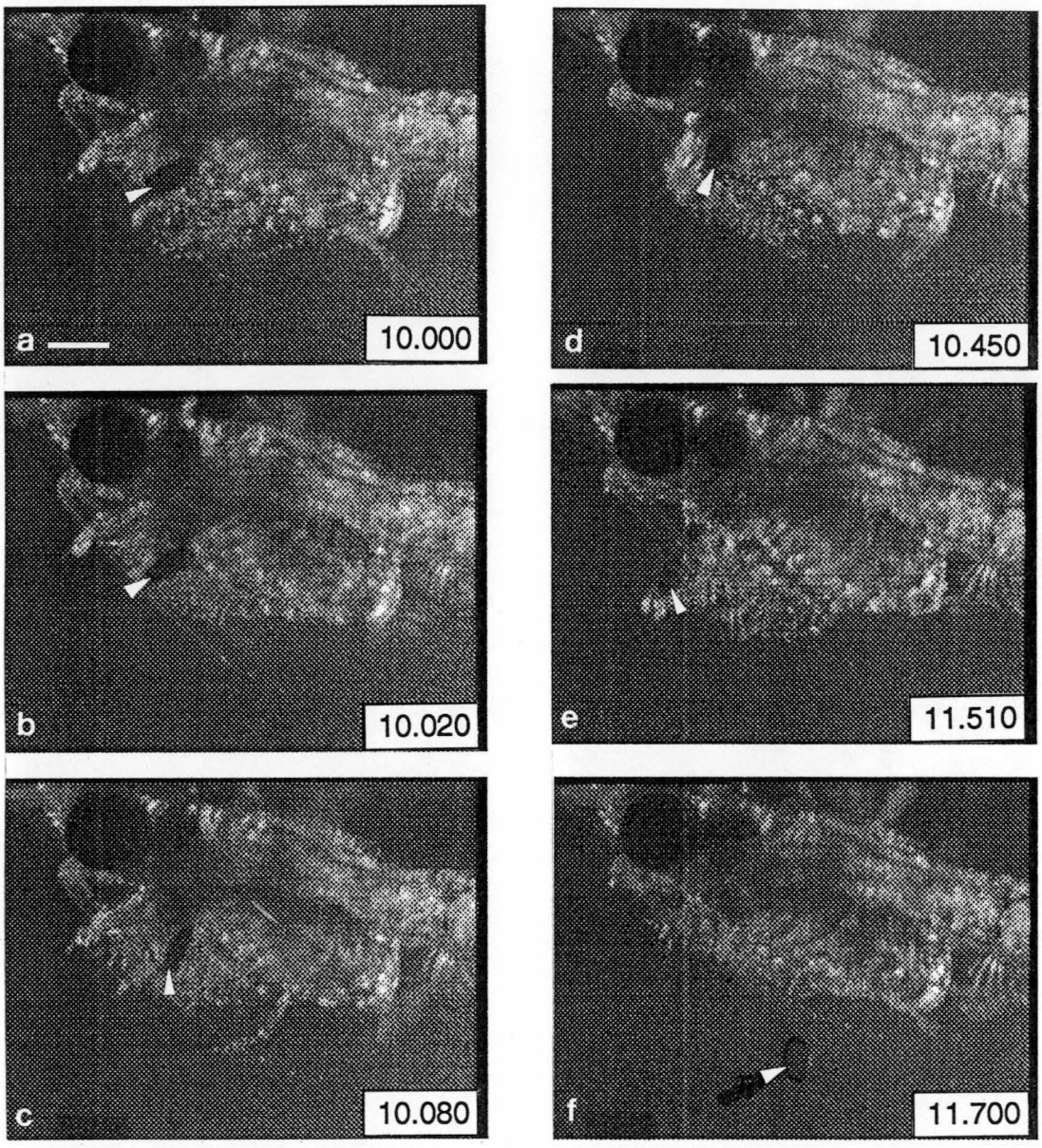
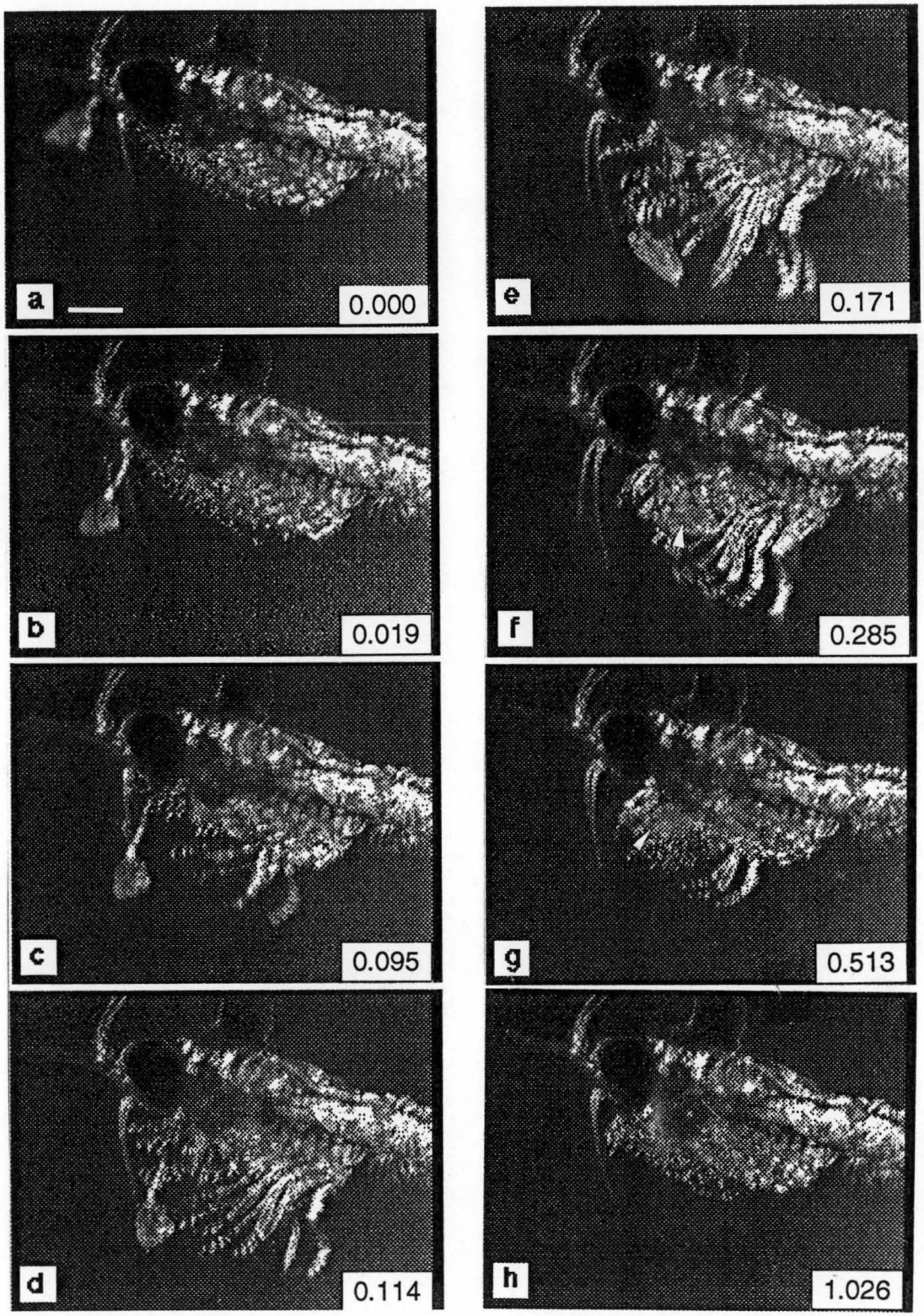

a
10.000
b
10.020
c
10.080
d
10.450
e
11.510
f
11.700

Figure 4.5 A series of video tape frames showing the capture of a juvenile *Daphniopsis australis* by an immature female *Paramesopodopsis rufa.* Scale bar (frame a) is 0.6 mm long. The number in each frame is elapsed time in s. Arrow heads in frames f and g point the prey.


a
0.000
b
0.019
c
0.095
d
0.114
e
0.171
f
0.285
g
0.513
h
1.026

anterior opening of the loose cage, the mandibular palps pushed the prey back inside the cage for continued chewing and ingestion. The frequency of biting the head region of the prey differed markedly from the frequency of biting the tail region first. Out of 30 successful capture and total ingestions, *P. rufa* ate 22 prey head first. Eating the head first involved biting either the dorsal portion of the head or either the left or right antenna.

During ingestion the exopods continued their rapid metachronal beat. E3 to E8 continued to form a cage, maintaining a streamlined body shape. *P. rufa* consumes its captured prey in its entirety. Rhythmic mandibular chewing and ocsophageal peristaltic movements were evident. The foregut of the stomach rhythmically expanded and relaxed. The exoskeleton of *D. australis* is darkly pigmented and when ingested it darkens the foregut of *P. rufa*. Soon after the complete ingestion of the prey, vigorous movements of E2 to E8 and autogrooming movements of the mouthparts followed (Fig. 4.1i). In instances where an adult ephippial female was ingested, *P. rufa* attempted to chew the oval-shaped ephippium, but to no avail; the ephippium was rejected or kicked away by the endopods (Fig. 4.4).

Anisomysis mixta australis

Prior to prey capture, *A. mixta australis* had its endopods adpressed on the underside of the thorax assuming a streamlined body shape (Fig. 4.6a,f). Upon approach of the juvenile *D. australis*, the endopods suddenly outstretched in a manner similar to that in *P. rufa* (Fig. 4.6b). Adult prey was not captured by *A. mixta australis*. The outstretching of the endopods was less sudden in this species mainly because of their relatively thinner limbs compared to those in *P. rufa*. The prey capture mechanism of *A. mixta australis* was very similar to that in *P. rufa*, in that the posterior endopods rapidly flicked the prey towards the anterior mouthparts. Both the primary and secondary cages were also used in this species in securing the captured prey during ingestion (Fig. 4.6c). Moving antennae and the cephalic region bearing the compound eyes of the prey were also often bitten first. While the mandibles

Figure 4.6 A series of video tape frames showing the capture and ingestion of juvenile *Daphniopsis australis* by a mature female *Anisomysis mixta australis*. Scale bar (frame a) is 0.6 mm long. The number in each frame is elapsed time in s. Arrow heads in frames b and c point the prey.

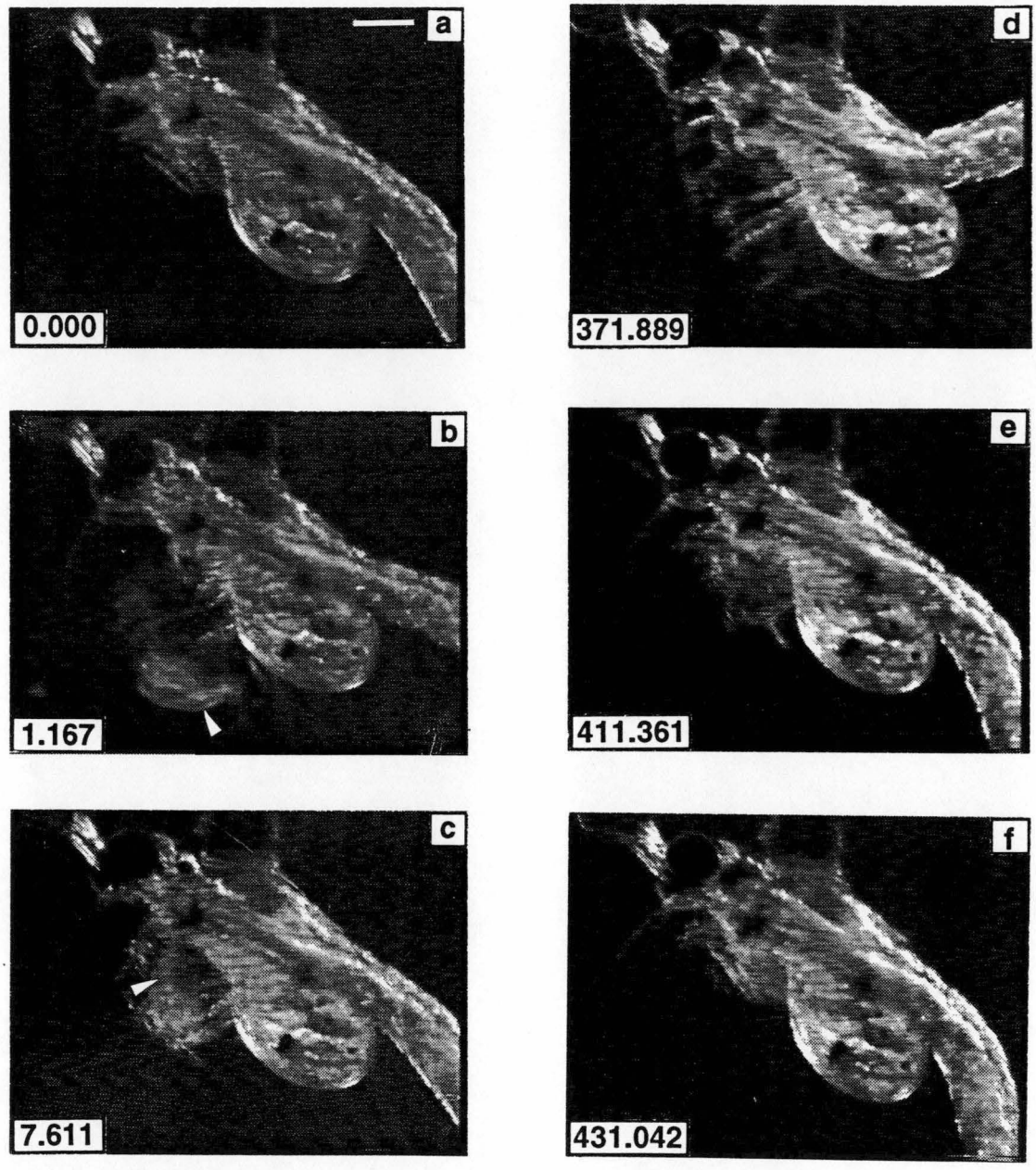

a
0.000
d
371.889
b
1.167
e
411.361
c
7.611
f
431.042

Figure 4.7 A series of video tape frames showing the capture and ingestion of a juvenile *Daphniopsis australis* by a mature female *Tenagomysis tasmaniae*. Scale bar (frame a) is 0.6 mm long. The number in each frame is elapsed time in s. Arrow heads in frames b-d point the prey.

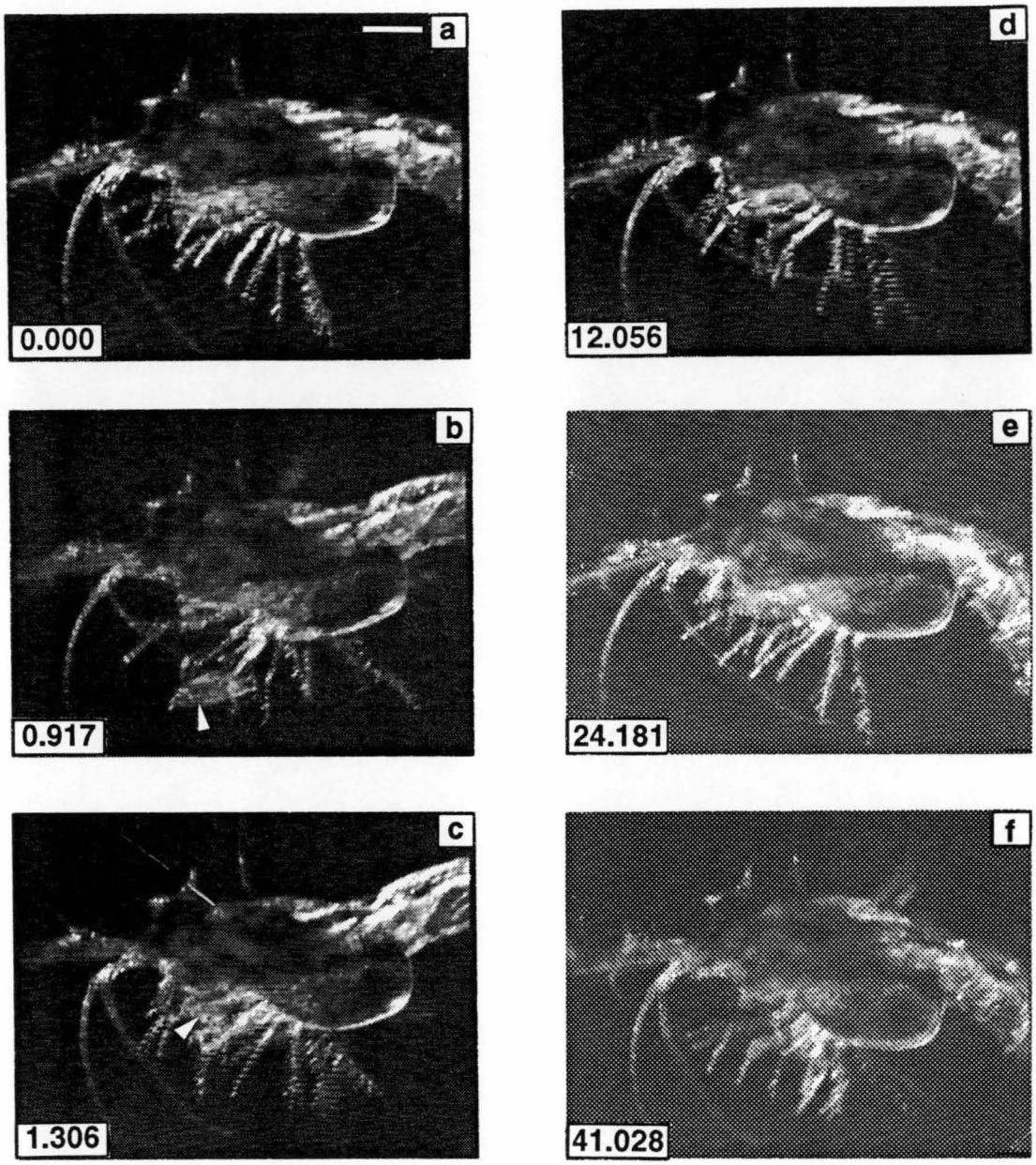
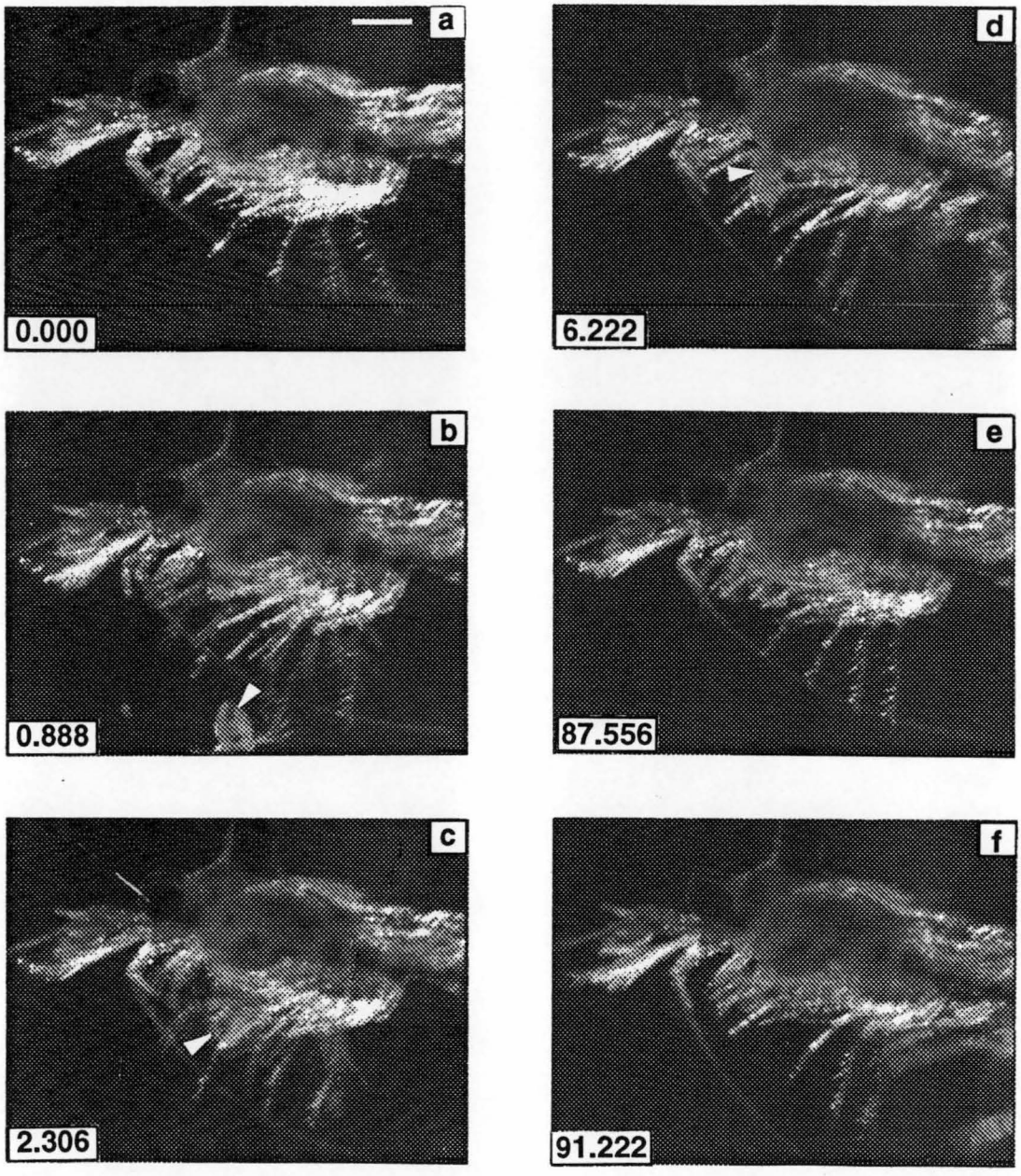

a
0.000
d
12.056
b
0.917
e
24.181
c
1.306
f
41.028

Figure 4.8 A series of video tape frames showing the capture and ingestion of juvenile *Daphniopsis australis* by a mature male *Tenagomysis tasmaniae*. Scale bar (frame a) is 0.6 mm long. The number in each frame is elapsed time in s. Arrow heads in frames b-d point the prey.


a
0.000
d
6.222
b
0.888
e
87.556
c
2.306
f
91.222

chewed, the rest of the mouthparts of *A. mixta australis* moved in a scissor-like manner on the bitten portion of the prey. *A. mixta australis* differs from the other two species in that it did not consume the entire prey, but most often rejected portions of the prey's carapace. Rapid autogrooming of the mouthparts and endopods similar to those in other two species concluded predatory feeding in *A. mixta australis* (Fig. 4.6d,e).

Tenagomysis tasmaniae

This species is different from the other two in that its endopods remained spread during the observation period (Figs. 4.7, 4.8). Upon rapid exopodal movements in female subjects, endopods were then loosely adpressed on the underside of the thorax. This gave a fairly streamlined body shape to the animal. The males in this species possess a complete set of pleopods (Fig. 4.8d,f), and the occasional burst of metachronal movement of both these limbs and the exopods brought the anterior four pairs of endopods tightly adpressed on underside of the thorax (Fig. 4.8f). Apart from the active anteroposterior paddling of the ventrally stretched E2, the approach of the prey brought the lower three podomeres of endopods 3 to 8 to a rapid fling and clap motion. Either E2 or these podomeres reached for the prey leading to a successful capture (Figs. 4.7b, 4.8b). If captured by the endopods, the prey was then serially tossed towards E1 and E2 which both gripped the prey while the mandibles chewed. During prey ingestion, the posterior endopods remained spread, thus *T. tasmaniae* primarily utilized the primary cage in restraining the prey (Figs. 4.7c, d; 4.8c,d). After entirely consuming its prey, the mouthparts and endopods of *T. tasmaniae* autogroomed as in the other two species (Figs. 4.7e, 4.8e).

Limb Outstretching Velocities and Prey Capture, Ingestion, and Handling Times

The highly significant variation ($F = 4.468$, df = 6, $p < 0.01$) between limb velocities of the outstretching endopods before the actual prey capture by *A. mixta*

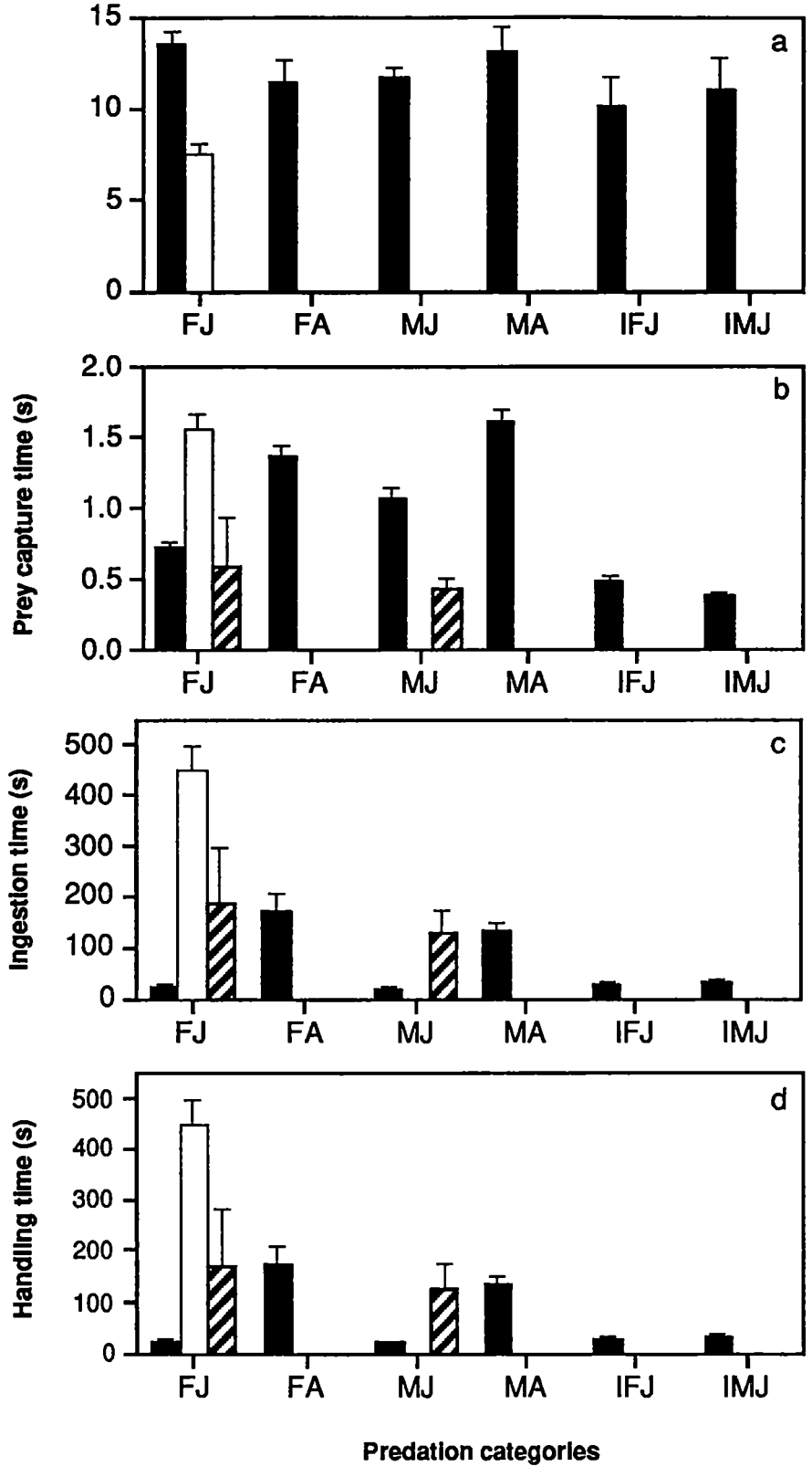


Figure 4.9 Variations in prey pre-capture limb velocities, and prey capture, ingestion, and handling times in three co-occurring mysid species. See Table 4.1 for the meaning of abbreviations of the different categories. Error bars - standard error. Open bars - *Anisomysis mixta australis*, solid bars - *Paramesopodopsis rufa*, hatched bar - *Tenagomysis tasmaniae*.

australis and *P. rufa* is shown in Figure 4.9a. Means of all 6 predation categories in *P. rufa* showed no significant difference ($p >> 0.05$). The lowest limb velocity recorded was 6.25 mm s^{-1} by an immature male mysid capturing a juvenile prey and the maximum limb velocity obtained was 16.45 mm s^{-1} by an adult male mysid capturing an adult prey. Outstretching limb velocities were only recorded in mature females of *A. mixta australis*. These values were comparable to those in all stages of *P. rufa* ($p > 0.05$), except those for female *P. rufa* capturing the juvenile prey and male *P. rufa* capturing adult prey ($p < 0.01$ for both) . No limb velocity was recorded from *T. tasmaniae* obviously because it did not show the sudden endopod outstretching shown by the other two species.

The time from the point of contact up to the time the prey is brought to the primary cage or prey "capture" time (Fig. 4.9b) varied significantly between predation categories and between mysid species ($F = 7.8$, df = 8, $p < 0.001$). No significant difference was found between all predation categories in *P.rufa* suggesting "capture" times for adult prey were the same as those for juvenile prey. There were also no significant differences between mature females and males mean capture times for adult and juvenile prey ($p > 0.05$ for all). However, if *P. rufa* results are analyzed alone, a bias becomes apparent due to the manner prey were introduced to the mysid. During the introduction, adult or juvenile prey which happened to be close to the anterior thoracic limbs of the tethered mysid were brought to the mouth region much faster than those prey which came in contact with the posterior endopods. Average prey capture time for juvenile *D. australis* was similar for all mature and immature mysids ($p > 0.05$). The shortest prey capture time was 0.19 s for an immature male capturing a juvenile prey while the highest value was 2.24 s for a mature female capturing an adult prey. Mature females of *A. mixta australis* captured the juvenile prey at a duration comparable to that for both mature stages of *P. rufa* capturing an adult prey ($p >> 0.05$), but their prey capture times were much longer compared to all *P. rufa* stages capturing juvenile prey and to the two stages in *T. tasmaniae* also capturing the juvenile prey ($p < 0.05$). Prey capture times for both male and

female *T. tasmaniae* were similar ($p > >0.05$). These values were comparable to all stages of *P. rufa* capturing juvenile prey ($p > 0.05$), but shorter than those for mature *P. rufa* capturing adult prey ($p < 0.05$).

P. rufa prey ingestion time (Fig. 4.9c) also showed a considerable variation ($F = 15.10$, df = 8, $p < 0.001$). This is partly due to the fact that mean ingestion times by mature *P. rufa* for adult prey were much longer than for juvenile prey ($p < 0.01$ for all). Average ingestion times for juvenile prey were similar for all mysid stages ($p >> 0.05$). Average time to ingest adult prey was also comparable between mature male and female *P. rufa* ($p >> 0.05$). The shortest ingestion time for adult prey was 97 s by a mature female and the longest was 292 s also by a mature female. Trends in *P. rufa* prey handling time (Fig. 4.9d) were similar to its prey ingestion time component, obviously because ingestion time values were much higher than capture time values. The anomalies in the prey capture time results disappeared when both capture and ingestion times data were added to give prey handling time by mysids. Mature females of *A. mixta australis* ingested the juvenile prey an order of magnitude slower than those in the different *P. rufa* stages ingesting a similar prey instar ($p < 0.001$). Their average ingestion time was two-fold longer than those for both mature females and males of *P. rufa* ingesting the adult prey ($p < 0.05$). The average ingestion time of mature female *T. tasmaniae* for the juvenile prey was two-fold shorter than those in mature females of *A. mixta australis* ($p < 0.05$), but comparable to both mature stages of *P. rufa* ingesting the adult prey ($p > 0.05$). The two stages of *T. tasmaniae* ingested the juvenile prey at a similar rate ($p > > 0.05$), but their ingestion times ranged from a two-fold to an order of magnitude faster than those of *P. rufa* stages ingesting the juvenile prey ($p < 0.05$). The handling times reflected the same pattern as those in the ingestion times in all predation categories of both *A. mixta australis* and *T. tasmaniae*.

Throughout the functional response experiments, similar sizes of *P. rufa*, *T. tasmaniae*, and *A. mixta australis*, and the different prey types were used (see Table 4.3) (CV within species < 5%).

Table 4.3 Predator and prey sizes in the functional responses experiments.

Predator	Predator total length (mean ± SD mm)	Prey	Prey total length (mean ± SD mm)
Anisomysis mixta australis	6.08 ± 0.15, n = 16	*Daphniopsis australis*	0.83 ± 0.08, n = 92
	6.04 ± 0.13, n = 20	*Gladioferens pectinatus*	0.81 ± 0.01, n =63
	6.43 ± 0.41, n = 20	*Artemia* sp.	0.75 ± 0.09, n = 40
Paramesopodopsis rufa	9.45 ± 0.31, n = 16	*D. australis*	0.93 ± 0.12, n = 92
	9.83 ± 0.46, n = 20	*G. pectinatus*	0.81 ± 0.01, n =63
	9.00 ± 0.60, n = 20	*Artemia* sp.	0.83 ± 0.04, n = 40
Tenagomysis tasmaniae	7.88 ± 0.37, n =16	*D. australis*	0.95 ± 0.10, n = 92
	7.85 ± 0.68, n = 16	*G. pectinatus*	0.81 ± 0.01, n =63
	7.41 ± 0.54, n = 20	*Artemia* sp.	0.80 ± 0.01, n = 40

Functional Response to *Gladioferens pectinatus*

Very low predation rates were recorded for mature *P. rufa* feeding on adult calanoid copepod prey, *G. pectinatus* (see Table 4.4). Predation rates in this largest mysid species ranged from 0.17 ± 0.4 SD at a prey concentration of 10 L^{-1} to 0.8 ± 1.3 SD at the highest prey concentration of 40 L^{-1}. *P. rufa* predation rates on *G. pectinatus* were lower compared to the other prey types. No captures were recorded in the other two mysid species (Table 4.4).

Table 4.4 Predation by the three mysid species on the calanoid copepod *Gladioferens pectinatus*. Data in mean ± SD.

Mysid species	Initial prey density (L^{-1})	Ingestion rate (*G. pectinatus* eaten mysid^{-1} h^{-1})
Anisomysis mixta australis	5	0
	10	0
	15	0
	20	0
Paramesopodopsis rufa	5	0.17 ± 0.04
	10	0.50 ± 0.8
	15	0.50 ± 0.8
	20	0.83 ± 1.3
Tenagomysis tasmaniae	5	0
	10	0
	15	0
	20	0

Functional Response to *Artemia* sp. Metanauplii

A highly significant variation was shown in the linear functional response curves of the three mysid species preying upon *Artemia* sp. metanauplii ($F = 6.26$, df = 50, $p = 0.001$). The predation rate values in *P. rufa* were lower than those in *T. tasmaniae* ($p < 0.001$), but comparable to *A. mixta australis* ($p > 0.05$). The predation rates on *Artemia* sp. metanauplii by *T. tasmaniae* were double than those by *P. rufa* and *A. mixta australis*. All three species showed an increasing linear curve against increasing prey concentration (Fig. 4.10A).

The lowest average predation rate for *A. mixta australis* was 0.36 ± 0.08 SE metanauplii mysid^{-1} h^{-1} at the lowest prey density (Fig. 4.10A). *A. mixta australis* predation rates varied significantly over the increasing prey concentration ($H = 8.67$, df =3, $p < 0.05$). The maximum predation rate of 1.77 ± 0.43 SE was recorded at the second highest prey concentration of 30 L^{-1}. The mean predation rate at this prey concentration was only significantly different from those at the two lowest prey concentrations ($Q < 0.05$), while for the rest of the treatments, means were not significantly different ($Q > 0.05$ for all).

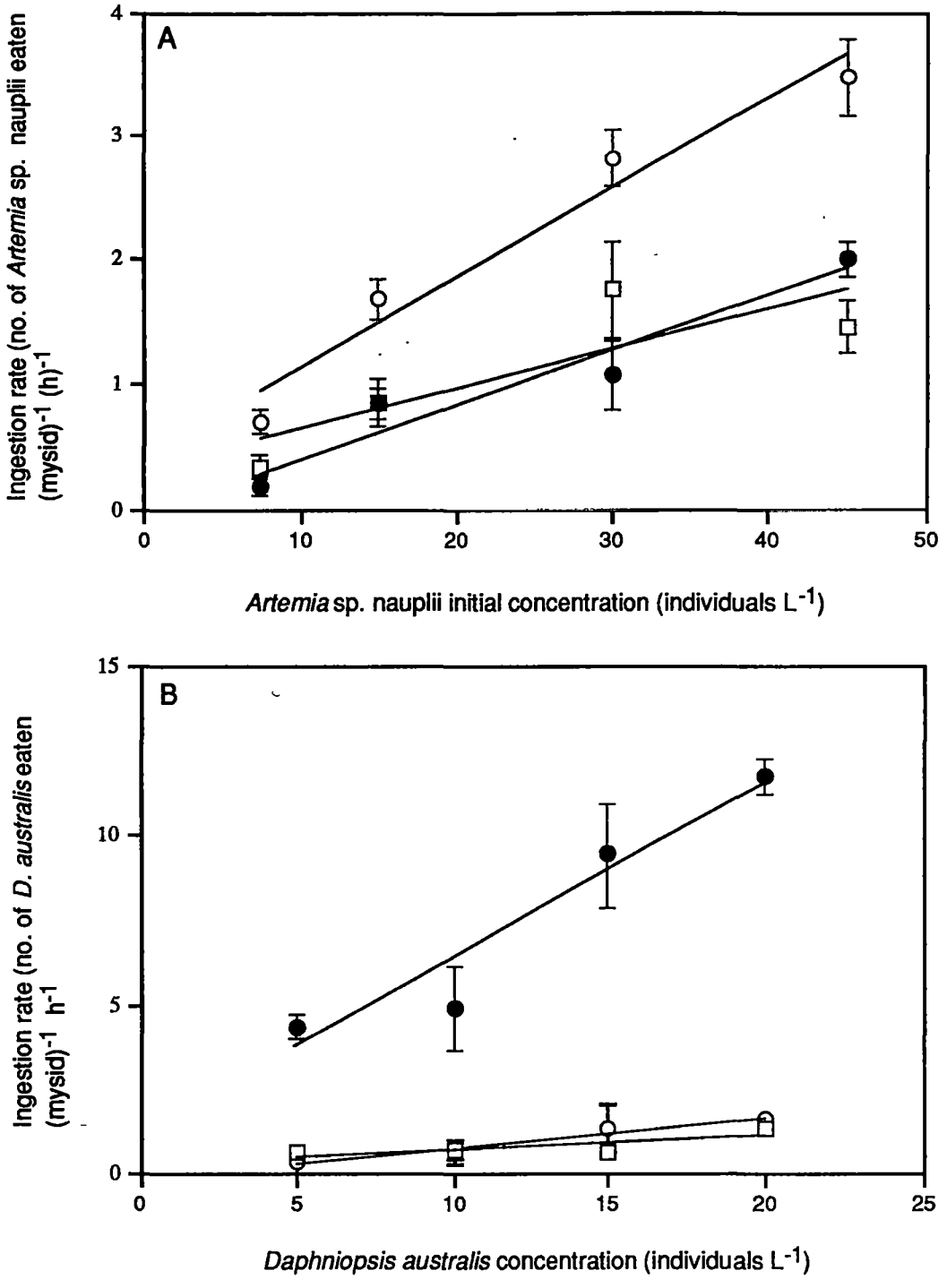


Figure 4.10 Functional response curves for the predation rates of the three mysid species feeding on two types of branchiopodan prey. A. *Artemia* sp. metanauplii, B. *Daphniopsis australis* juveniles. Error bars: standard error. Squares - *Anisomysis mixta australis*, closed circle - *Paramesopodopsis rufa*, open circle - *Tenagomysis tasmaniae*.

The average predation rates by *T. tasmaniae* also increased with increasing *Artemia* sp. metanauplii concentration with a minimum of 0.7 ± 0.08 SE and reaching

a maximum of 3.5 ± 0.33 SE at 45 L^{-1} (H = 16.65, df = 3, $p < 0.01$) (Fig. 4.10A). The predation rate in the highest prey concentration differed significantly from that in the lowest prey concentration ($Q < 0.005$), but was similar to the second highest prey concentration ($Q > 0.05$). The latter was also significantly different from the predation rate at the lowest prey concentration ($Q < 0.05$), but not with that at the second lowest prey concentration ($Q > 0.05$). The predation rates at the two lowest prey concentration were similar ($Q < 0.05$).

The average predation rates by *P. rufa* on *Artemia* sp. metanauplii followed a linear relationship with increasing prey concentration, and these values varied significantly (H = 14.25, df = 3, $p < 0.05$) (Fig. 5.10A). Predation rates of *P. rufa* ranged from 0.2 ± 0.06 to 2.0 ± 0.13 *Artemia* sp. metanauplii $mysid^{-1}$ h^{-1}. The predation rate at the highest prey concentration differed significantly only with that at the lowest prey concentration ($Q < 0.05$). The rest of the rates at the other prey concentrations were similar ($Q < 0.05$ for all).

Functional Response to *D. australis*

At the lowest prey density, average *P. rufa* ingestion rate was 4 ± 0.29 prey $mysid^{-1}$ h^{-1}, and it continued to increase with increasing prey density to a maximum ingestion rate of 11.75 ± 0.48 prey $mysid^{-1}$ h^{-1} at 20 L^{-1} density (Fig. 4.10B). Dissected mysid foreguts revealed 100 % fullness while those with very low ingestion rates showed 30% to 50% fullness. *Paramesopodopsis rufa* ingestion rates varied significantly with increasing prey density (H = 14.25, df = 3, $p < 0.01$), although those at 5 and 10 L^{-1} were the same ($Q > 0.05$). This is because two out of the four mysids fed at 10 L^{-1} treatment density and 1 out of the four mysids at 15 L^{-1} gave relatively very low (0.5 and 3 prey $mysid^{-1}$ h^{-1}, and 2.5 prey $mysid^{-1}$ h^{-1}, respectively) ingestion rates. These mysids were mature females without young in their brood pouches, and perhaps were about to moult. Mysid ingestion rates at the two higher prey densities differed significantly ($Q < 0.05$) from the two lower prey densities, but ingestion rates between the two higher prey densities were similar ($Q > 0.05$). The functional response curve of *P. rufa* to increasing density of juvenile *D. australis* is

linear (Fig. 4.10B).

Increasing density of *D. australis* did not increase predation rates in *T. tasmaniae* (Fig. 4.10B) ($H = 16.66$, df = 3, $p > 0.24$). Very few individuals captured the prey. The lowest successful predation rate was 1 prey mysid^{-1} h^{-1}, and the highest was 3. Averages from the four prey density treatments ranged from 0.75-3.25 prey mysid^{-1} h^{-1}.

As with *T. tasmaniae*, very few *A. m. australis* captured the prey. A predation rate of 0.5 prey mysid^{-1} h^{-1} was the lowest, and the highest was 2. Increasing prey density did not increase predation rates ($H = 4.13$, df = 3, $p > 0.24$), and the average ranged from 1.25-2.75 prey mysid^{-1} h^{-1}.

The functional response curves to the different *D. australis* concentrations by the three mysid species differed significantly ($F = 49.86$, df = 45, $p < 0.001$). The variability was attributed to the significantly higher predation rates by *P. rufa* compared to those in the other two species ($p < 0.001$). The predation rates of *A. mixta australis* and *T. tasmaniae* showed no significant difference ($p > 0.05$).

Discussion

Predatory Feeding Mechanism

Mysids may detect prey by single or combined mechanisms of vision (Ramcharan & Sprules 1986), mechanoreception or chemoreception (Crouau 1989). However prey detection is done, mysids both passively and actively encounter their prey. A passive encounter is when a prey is seized only when brought near the endopods by the strong exopod currents (Cooper & Goldman 1980; Siegfried & Kopache 1982). In contrast, active encounter and subsequent prey capture involves a short (usually < 1 cm) forward or sideways lunge (Ramcharan *et al.* 1985) or the animal darting forward (Wooldridge & Bailey 1982). The anteriorly oriented attack by immature and mature stages of free-swimming *P. rufa* on juvenile *D. australis* includes an upward tilting of its body

pitch 45 to 50 degrees relative to the horizontal plane .

Fuzessery and Childress (1975) described a concerted endopod extension by the deep sea mysid *Gnathophausia ingens* as a feeding response to various chemical stimuli. They suggested that the response is a way of entrapping prey against the ventral body surface. Likewise, Schabes and Hamner (1992) noted that the endopods of three shallow water mysids are extended in an open basket configuration typical of the capture of large particles. In *P. rufa*, similar stereotyped outsplaying of limbs was observed upon approach of either juvenile or adult *D. australis*. Frame by frame analysis of this limb posture showed sudden and concerted flinging of the second to the eighth pairs of endopods, apparently sucking the prey towards the outstretched limbs. Although not quantified, low Reynolds number (<1) operates in these thoracic limbs, and simultaneous outflinging would certainly generate some degree of suction (Strickler 1984).

The capture and manipulation of large food particles by mysids have been previously reported to involve all thoracic endopods (Depdolla 1923; Cannon & Manton 1927). My filming observations of a highly magnified anterior half of the three species further extend these observations. The actual grasping and capture of a daphniid prey by these mysid species primarily involves the more anterior limbs, *viz*. the second and third pairs of endopods. More posterior endopods assume no capturing role, but if the prey happens to touch these limbs first, the prey is tossed towards the capturing anterior limbs. Soon after contact, these limbs bring the prey medially towards the first pair of endopods which then securely clasp the prey. The major role of mandibular palps and the first two pairs of thoracic endopods in the manipulation of large food particles has been emphasised by Mauchline (1980). This is further reinforced by the more detailed descriptions of the present study as aided by the micro-videographic technique and the tethering procedure for keeping mysids at a fixed position. The three species never grip their prey in between the mandibular palps as noted by Cannon & Manton (1927), but the mandibular palps function as an anterior cover of the

cage, and prevent prey from escaping through this region. It was then recognized that a primary cage comprising these limbs and the other mouthparts is formed by the three mysid species.

The secondary cage formation of endopods in mysids has already been reported to follow prey capture (Siegfried & Kopache 1982; Wooldridge & Bailey 1982). The endopods 3 to 8 of both *A. mixta australis* and *P. rufa* form most of the cage assuming a hydrodynamically effective body shape, and secure the prey in place during ingestion. This cage was not observed in *T. tasmaniae* in which the endopods remained spread most of the time. Its habit of resting on or a few centimetres above the sandy substrate (Fenton 1992; O'Brien 1987) might explain this characteristic behaviour.

In mature and immature stages of *P. rufa*, very rapid repositioning of prey occurred, often initiated by the beating of the antennae, resulting in the head of the prey being eaten first. This was also observed in the other two species. Mature females of the calanoid copepod *Euchaeta elongata* eat moving parts of the prey first, such as the first antennae and/or urosome (Yen 1983). On the contrary, Siegfried & Kopache (1980) reported that *Neomysis mercedis* consumed prey either anterior or posterior region first, suggesting equal chances of these prey parts being eaten first. However, they did not provide further details of their observations. In vertebrate predators, prey mutilation involving the head or neck being bitten first severs the main motor centers of the head thereby paralysing the prey (Curio 1976). Among invertebrate predators, squids capturing a fish prey cut the flesh of the neck deeply enough to penetrate the spinal cord (Verrill 1880 cited in Bradbury & Aldrich 1969). In *P. rufa*, the higher frequency of head being eaten first suggests this behaviour as a way of immobilising *D. australis* for easier subsequent ingestion.

This study for the first time reports evidence of a mysid attempting to ingest an ephippium of a daphniid. The ephippium was bitten several times by the mandibles but later on rejected. Ephippia, being dormant stages in daphniids, are made of tough chitinous coatings and are a means of population dispersion

because they resist harsh environmental conditions and only hatch when favourable conditions prevail (Fryer 1991). The present observation shows that they are also resistant to the powerful chewing of the mysid mandibles.

Instances of smaller or immature *P. rufa* not capturing adult *D. australis* are experimental artefacts of the current study. Immature mysids have been reported to ingest adult or large size *Daphnia* (Cooper & Goldman 1980; Murtaugh 1981a,b). However, they are not as efficient at this as adult mysids. Murtaugh (1981b) noted that smaller *M. relicta* ingest prey at much reduced rates compared to adults. Lasenby *et al.* (1986) derived a predation rate function using Bowers & Vanderploeg's (1982) equation for *M. relicta* preying upon adult *Daphnia* sp. showing smaller mysids to feed at one third the rate of larger individuals.

Outstretching limb velocities by mysids are similar in immature and mature stages of *P. rufa*, and range from 6.25 to 16.45 mm s^{-1}. These limb velocity values are high enough to be very effective in capturing a slow swimming daphniid prey. Although the actual swimming speeds of juvenile and adult *D. australis* were not quantified, values reported from other daphniids would be comparable. *Daphniopsis pusilla*, which shows very similar general body form and behaviour to that of *D. australis*, swims and feeds in the manner of *Daphnia*, and exhibits a *Daphnia*-like body orientation (Fryer 1991). Average normal swimming speeds of *Daphnia* range from 1.5-5 mm s^{-1} at 15°C (Gerritsen 1982). Ignoring body thrust during attack by an individual mysid, just the outstretching limb posture alone would be effective in capturing *D. australis*. However, reported swimming speeds would be much higher in an escaping *Daphnia* and would contribute to a diminished capture success by its predator. This is consistent with our aquarium observation of a free swimming *P. rufa* not readily capturing an evading *D. australis*. Active evasion by *D. australis* involves diving down to the bottom or swimming away from the approaching predator, a similar active escape behaviour shown in *D. pusilla* (Fryer 1991). Furthermore, it would be very simplistic to derive successful prey capture in *P. rufa* from its

limb velocities alone. Although these limb velocity values indicate a high potential for contributing to prey capture success, individual prey escape behaviour and predator avoidance strategies which lessen predator capture success need to be considered (Ohman 1988; Gliwicz & Pijanowska 1989). The relatively thinner endopods of *A. mixta australis* (see chapter on mouthparts morphology) compared to those in *P. rufa* explain the lower limb velocity during outstretching.

Prey capture time is shorter than prey ingestion time because of the quick manner in which the three mysid species bring their prey to the mouth region. Immediately on capture the prey is pushed by the first and second pairs of endopods and mouthparts to the mandibles for biting and ingestion. Size of prey clearly affects ingestion time. Mature and immature *P. rufa* took an average of 21.2 s to ingest juvenile *D. australis* while mature *P. rufa* took an average of 220 s to ingest adult *D. australis*. Ramcharan *et al.* (1985) reported that for *M. relicta* the average handling time (measured from the moment of capture to the unfolding of the endopods at the end of ingestion) for *Daphnia pulex* with average size of 1.07 mm ± 0.21 SD was 96.9 s. Even if we add the maximum prey capture time of 2.1 s and the average actual ingestion time of 21.2 s, *P. rufa* average handling time for juvenile *D. australis* of average size (0.85 mm ± 0.14 SD) comparable to that of *D. pulex* would still be much shorter than in *M. relicta*. The difference in morphology of prey species may explain this disagreement. *D. pulex* possesses a caudal spine absent in *D. australis*, and prey specialisations like bodily projections have been implicated as a prey evolutionary strategy to increase handling time (Ohman 1988). Fryer (1991) believes that the absence of a caudal spine in the genus *Daphniopsis* is an adaptation to a predator-free habitat and such bodily projections are no longer important.

The effect of size of predator is clearly shown with *A. mixta australis* ingesting its prey much longer than the other two larger species. It is also worth mentioning that suction feeding on the prey's soft parts may be very important in the small-sized *A. mixta australis* as it did not completely consume its prey but

discarded exoskeleton parts. This mode of feeding could not be attributed to being small in size because suction feeding has also been reported in the large mesopelagic mysids, *Petalophthalmus armiger* and *Longithorax fuscus* (Tchindonova 1959 and Vinogradov 1962 cited in Mauchline 1980). Mauchline and Fisher (1969) also noted this behaviour among euphausiids feeding on copepods. The other two species showed comparable whole prey ingestion times at similar prey size suggesting similar efficiency in mechanical trituration of prey.

Techniques such as micro-videography have proved to be highly useful for gaining a detailed picture of the neglected field of zooplankton behaviour particularly understanding and quantifying the different components of Holling's (1959a,b) predation framework (Price 1988). The other components of *P. rufa* predation involving the encounter and pursuit of prey should be addressed in similar future studies.

Functional Response to Prey Density

The functional response of predators may be classified into types I, II, and III (Holling 1959a,b). The type I or rectilinear response is characterized by a linear increase in consumption rate up to a certain prey concentration where the rate suddenly reaches a plateau and stays at zero with further increases in prey concentration. This is exemplified by filtration rate of filter feeders such as daphniids (Rigler 1961), and calanoid copepods (Frost 1972). The type II or exponential response is an initial proportional increase with increasing prey concentration which gradually decreases as "saturation" level of prey concentration is approached; beyond this predation rates remain stationary with further increase in prey concentration as in the type I functional response. These two types of responses have been considered destabilizing to predator-prey interactions because of the capacity of the prey to damp predation rates by simply increasing its density. In addition, at low prey density, predators could drive prey populations to extinction. This contrasts with the type III functional response in which predation rate remains low at low prey concentration and starts to

increase at a certain higher prey density. The type III functional response is stabilising to the predator-prey interaction and is characterized by a sigmoid type of curve.

A Type II functional response curve is commonly observed among invertebrate predators (Holling 1965). A Holling type II has been reported in *M. relicta* preying upon the copepod *Epischura*, but a Holling type III functional response was shown for another copepod prey *Diaptomus* (Folt *et al.* 1982). Fulton (1982) reported a type II curve from laboratory experiments on *Mysidopsis bigelowi* preying upon *Acartia tonsa*. In contrast, a similar laboratory predation experiment involving *M. relicta* and *Epischura* collected from a different location showed a linear functional response (Cooper & Goldman 1980). Estimation of *M. relicta* predation rates from field samples showed a similar linear type of curve which was attributed to food limitation (Bowers & Vanderploeg 1982). These differences in mysid functional response have been attributed to prey vulnerability which varies according to prey types and their escape abilities (Folt *et al.* 1982; Fulton 1982; Ohman 1988; Yen 1983; McClatchie 1988), predator hunger and feeding physiology (Yen 1983), aggregative behaviour of both prey and predator (Folt 1985; O'Brien & Ritz 1988), and temperature (Fulton 1983).

The three mysid species were not efficient at capturing adult *Gladioferens pectinatus*. This is contrary to some reports on other mysid species which showed high capturing efficiency for adult calanoid copepods (*e.g.* Mauchline 1980; Fulton 1982b; Wooldridge and Bailey 1982). However, other studies have also reported mysid species which are inefficient at capturing adult calanoid copepods (*e.g.* Siegfried and Kopache 1980). The prey species used may explain differences in results. Low predation rates have been associated with the extremely agile and fast swimming attributes of adult calanoid copepods (Fulton 1982; Yen 1980; Greene and Landry 1985; Ohman 1988). The high frequency of this food type from gut content analysis may be attributed to the fact that estuarine mysids, being scavengers or necrophagous feeders, might be eating younger calanoid stages with weak escape motility (not tested in the present study) or moribond adult calanoid copepods.

The predation rates by the three mysid species with increasing *Artemia* sp.

metanauplii concentration ranged from 0.2 to 4 prey mysid^{-1} h^{-1}. The three species showed higher predation rates of 0.8 to 3 prey mysid^{-1} h^{-1} at 15 to 30 prey L^{-1} compared to those reported by Stuart and Hugget (1992) of 0.54 to 0.83 prey *Euphausia lucens*$^{-1}$ h^{-1} at 20 *Artemia* sp. nauplii (of comparable body length with the present study) L^{-1}. Differences in the prey capturing mechanisms between mysids and euphausiids may explain these results. Mullin and Roman (1986) fed *Anisomysis* sp. with 100 to 1000 Artemia nauplii L^{-1} and obtained a range of 1 to 6 nauplii mysid^{-1} h^{-1}. The mysid species they studied is comparable in terms of body length with *A. mixta australis* which at 45 prey litre showed a predation rate range of 0.3 to 3 nauplii mysid^{-1} h^{-1}. The functional responses by the three mysid species to increasing *Artemia* sp. concentration generated were all linear. The linear responses shown by the three species do not match any of Holling's functional response models. This is attributed primarily to the considerable variability of predation rates. On the other hand, the linear responses probably indicate that the initial concentrations of prey are well below threshold levels. If this is valid then the functional responses obtained in the present study might form the linear portion of the rectilinear (type I) or perhaps the curvilinear (type II) models below the critical concentration of prey.

Linear functional responses best describe predation on juvenile *D. australis* by the three mysid species. Similar explanations as those responses for the *Artemia* sp. metanauplii are invoked.

Paramesopodopsis rufa predation rates on *Artemia* sp. metanauplii were lower than on the juvenile stages of *D. australis*. The differences in the swimming patterns and body shape of these two branchiopodan prey species may strongly influence predation rates by *P. rufa*. The predation rates by the two other mysid species for both *D. australis* and *Artemia* sp. metanauplii were similar indicating that predation rates in this case are not affected by the two prey types. The functional responses for *T. tasmaniae* and *A. mixta australis* were a simple line like that in *P. rufa*.

Aside from predator size, results here suggest that mysid species differ in the actual prey handling process as suggested from predation rates. *P. rufa* feeding coefficient for juvenile *D. australis* is 44 L day^{-1} (calculated from a maximum ingestion

rate of 12 prey mysid^{-1} h^{-1} in a 2-litre predation chamber) which is more than twice the 20.2 L day^{-1} feeding coefficient reported by Ramcharan *et al.* (1985) in *M. relicta.* In comparison to these two mysid species, *T. tasmaniae* and *A. mixta australis* predation rates are still relatively low. Apart from the small size of *A. mixta australis*, its habit of feeding upon small particulate materials (Fenton 1986) may explain the low predation rates. *T. tasmaniae*, despite being larger than *A. mixta australis*, still showed comparable low predation rates. Most *T. tasmaniae* spent the two hour experimental period resting on the bottom of the jar reducing their chance of encountering the swimming *D. australis.* The fact that this species has been reported to be a substrate specialist (O'Brien and Ritz 1988) and showed predominantly macroalgal detritus in its diet (Fenton 1986) may explain the reduced predatory feeding performance.

Predation may not be limited by prey ingestion and handling time considering the very short duration associated with these processes. This conclusion, which is apparently true for *M. relicta* (Ramcharan *et al.* 1985), will be discussed in detail with particular reference to the apparently highly predatory *P. rufa* and the daphniid *D. australis* as prey. Using the average ingestion time of 0.37 min per juvenile *D. australis*, and the maximum ingestion rate (saturation point) of 12 prey mysid^{-1} h^{-1}, *P. rufa* would only spend about 4.40 min ingestion time plus 0.04 minutes capture time in an hour. Hence, if an individual *P. rufa* is offered juvenile *D. australis*, saturation point ingestion rates contribute only 7.4% of its time, while 92.6% perhaps is spent cruising, searching, pursuing, and attacking prey, or in other essential behaviour. Again, prey morphology and escape tactics/behaviour may partly explain this pronounced non-feeding period in *P. rufa.* Gerritsen & Strickler (1977) noted that although their model predicts that increased swimming speeds of a cruising invertebrate predator would mean increased encounter rate with its prey, this does not necessarily cause increased prey ingestion rates. This is so because in real situations prey escape abilities may reduce their chance of being ingested after encounters with predators.

Assuming adult *P. rufa* feeds on juvenile *D. australis* continuously within a day, our results if computed on a daily basis, would give daily ingestion rates ranging

from 96 to 288 prey mysid^{-1} day^{-1} (Table 4.5). *A. mixta australis* showed the lowest daily predation rate compared to all mysids listed but this is mainly due to size

Table 4.5 Maximum ingestion rates of daphniids by mysids in laboratory experiments.

Mysid species (Location) (Reference) (Size in mm)	Prey species	Initial prey density (L^{-1})	Chamber volume (L)	Duration (h)	Predation rate (prey mysid^{-1} day^{-1})
M. relicta (Lake Michigan) (Grossnickle 1978 cited in Bowers and Vanderploeg 1982) (14 - 17)	*Daphnia*	100.0 6.9	? ?	? 12	480.0 84.1
Mysis relicta (Lake Tahoe) (Cooper & Goldman 1980) (mean = 15.8)	*Daphnia pulicaria*	14.8	3	12	34.1
M. relicta (Gull Lake, Ontario) (Ramcharan & Sprules 1986) (mean = 18.6 ± 2.0)	*D. magna* *D. pulex*	40	10		120 - 125
Neomysis mercedis (Lake Washington) (Murtaugh 1981b) (9.6 - 10.2 for individuals preying upon *D. pulicaria* and *D. thorata*; 6.2 - 7.4 for individuals preying upon *D. pulex*)	*D. pulex* *D. pulicaria* *D. thorata*	148 298	2.8 0.15 - 4	1.2 - 6.2	32 89
Neomysis mercedis Lake Washington (Chigbu and Sibley 1994) (mean ± SE = 13.56 ± 0.13)	small *D. magna* medium *D. magna* large *D. magna*	25 15 15	2 2 2	12 12 12	60 37 25.6
Paramesopodopsis rufa Present study (9.1 - 10.3)	*Daphniopsis australis*	20	2	2	96 - 288
Tenagomysis tasmaniae Present study (7.10 - 8.75)	*D. australis*	20	2	2	24 - 72
Anisomysis mixta australis Present study (5.7 - 6.40)	*D. australis*	20	2	2	12 - 24

difference. The daily predation rate of *T. tasmaniae* is comparable to those of *Mysis relicta* ingesting *Daphnia pulicaria*, and those of *Neomysis mercedis* ingesting *Daphnia pulex*. The minimum value is fairly close to the *in situ* ingestion rate of 89 prey mysid^{-1} day^{-1} reported by Murtaugh (1981b) in *M. relicta*. The maximum ingestion rate is nearly half the value (480 prey mysid^{-1} day^{-1}) reported by Grossnickle (1978 cited in Bowers and Vanderploeg 1982) who used an initial prey density of 100 L^{-1} in a laboratory feeding experiment with *M. relicta*. Higher ingestion rates in *P. rufa* may be attributed to the motion introduced by the plankton roller during the feeding experiment. It is speculated that these water movements increase rates of encounter and successful capture by the mysid. The increased encounter rate between predator and prey due to water movements has been very recently reported (Kils 1992).

Although the majority of experiments were conducted in laboratory conditions, the studies described in this chapter have demonstrated that different mysid species show characteristic feeding behaviour in response to the various prey features. In the present study, the classical proportional increase of predation rate in response to prey availability is demonstrated. However, other prey characteristics, such as gross body shape, swimming movements, and perhaps palatability also influence the predatory feeding behaviour in the three co-occurring mysid species.

Various foraging strategies among competing predatory species may serve as means of achieving co-existence by resource partitioning (Begon and Mortimer 1986). Food resource partitioning mechanisms have been linked with reducing or minimizing overlap of the food resource utilization curves between competing species and at the same time balancing or offsetting the effects of intra-specific competition (Schoener 1974, 1989). In the case of the present study, the different predatory feeding behavioural response in the three mysid species to various prey types indicates a probable feeding niche dimension within which these three co-occurring mysid species partition.

CHAPTER 5

IN SITU FEEDING BEHAVIOUR STUDIES

Introduction

Pelagic organisms ultimately depend on a range of suspended food particles (Sierszen and Frost 1992). Food size seems to be the dominant factor in determining potential for exploitation, but other properties such as taste, nutritional value, electrical charge, concentration, and diversity may also play an important role in the feeding behaviour of these organisms (Paffenhøffer 1988). Suspension-feeding planktonic crustaceans normally encounter living particles such as bacterioplankton, phytoplankton and other zooplankters, which are usually outnumbered by non-living inorganic and organic particles collectively termed detritus. It has been recognized that the detritus itself is of limited nutritive value as a direct food source for animal life, primarily because of its indigestible plant and animal structural components (Foulds and Mann 1978; Kirby-Smith 1976; Mann 1988; Newell 1984). With the exception of some animals which possess complementary digestive enzymes, be they endogenously synthesized or manufactured by their resident gut microflora, the majority of pelagic detritivores rely on the epimicrobiota which conditions and increases the nutritive value of the detrital substrate (Foulds and Mann 1978).

As reviewed in chapter 1, shallow water mysids are generally omnivorous ingesting a variety of sestonic particles. Amorphous detrital materials often contribute the largest proportion in their diets. This might be expected in suspension feeding mysids which inhabit the detritus-rich estuarine/neritic waters. The three major inputs of detritus in the coastal/estuarine region are flocculent material formed by the utilization of dissolved organic matter (DOM) (*e.g.* through bacterial activity, precipitation, and adsorption), *in situ* production (*e.g.* from death, faeces of residents and immigrants, moults, messy feeding, non-viable eggs), and terrestrial, freshwater and marine external input (*e.g.* from horizontal transport, re-suspension of bottom

sediments) (Jumars *et al.* 1984). The detritus may play a valuable role in stabilizing the estuarine ecosystem by levelling out the seasonal variations in primary production, and ensuring a quick re-absorption of dissolved nutrients (Mann 1988). These detrital materials, which may either be a major source of nutrients to the inshore areas or just a nutritional supplement, are retained in the coastal waters and probably move parallel to the coast in a narrow band of turbid coastal waters or are retained in estuarine regions (Nixon 1986).

Within constraints of its limitations, the radiotracer technique, when used in trophic studies, has been shown to yield accurate estimates of *in situ* feeding rates (Roman and Rublee 1981; Paffenhøffer 1988). The technique of allowing incorporation of tritiated thymidine into bacterial DNA has proved to be sensitive in measuring clearance rates of microzooplankton feeding on bacteria (Hollibaugh *et al.* 1980). Use of the same ^{3}H-thymidine in labelling heterotrophic bacteria has yielded conservative estimates of bacterial production in the sea (Fuhrman and Azam 1982). Growth and production of phytoplankton may be accurately estimated from photosynthetic uptake of $NaH^{14}CO_3$ (see review by Carpenter and Lively 1980). Food selection studies among marine organisms have been achieved using the radiotracer technique. For example, Mullin (1983) measured filtering rates of the salp, *Thalia democratica*, on ^{3}H-thymidine-labelled bacteria and ^{14}C-labelled phytoplankton and found higher salp feeding rates on the latter food type. Food resource partitioning between three species of benthic copepods has been demonstrated by radio-labelling microbial prey: bacteria with ^{14}C-acetate, and photoautotrophs with $NaH^{14}CO_3$ (Carman and Thistle 1985). In a short term feeding experiment using Haney chambers, Roman and Rublee (1981) measured *in situ* zooplankton grazing rates on ^{14}C-labelled autotrophic and ^{3}H-labelled heterotrophic particulate matter, and reported a negative selection for ^{3}H-labelled particles. The importance of coral-mucus detritus as food for reef zooplankton, *Acartia tonsa* and the mysid *Mysidium integrum*, has been emphasized using a similar dual-labelling technique (Gottfried and Roman 1983). Recently, Mullin and Roman (1986) used similar techniques to examine *in situ* feeding rates of a coral reef mysid, *Anisomysis* sp., and noted that larger food particles

represented by the nauplii of *Artemia* sp. and algal detritus are more important than the smaller phytoplanktonic particles.

No study has been done on the feeding rates of the three co-occurring mysids described earlier on naturally occurring food items, thus their functional role in their habitat and the relative importance of the different food types in the diet remain unestablished. The aim of this study is to seek answers to questions: (1) Are the three mysids species selective when offered different types of food such as phytoplankton, zooplankton, and algal detritus? (2) What are their feeding rates on these food types?, (3) Do they vary their feeding rates and selectivity at different times of the year?, (4) Do they vary feeding rates and selectivity when held together?, and (5) What are the implications of the answers from (1) to (5) with regard to the feeding behaviour of the three mysid species? Answers to these questions will be based on *in situ* experiments performed as near to natural conditions as possible, with minimum disturbance to the animals.

Materials and Methods

Location of the Study

The study was conducted off Taroona Beach, 10 km South of Hobart, Tasmania (147° 21' East, 42° 57' South) (Fig. 5.1). The study area is located in a small embayment with Crayfish Point as the northern boundary of the mouth. The bottom is characterized by sandy sediment with patches of rock outcroppings which are covered with sessile animals and plants (mainly brown and red macroalgae). Under the classification of Edgar (1984), exposure of the area is sub-maximal to moderate . The waters are almost fully marine as the site is influenced by a salt-wedge year round (Taw and Ritz 1978). However, freshwater intrusion from the River Derwent results in brackish water conditions.

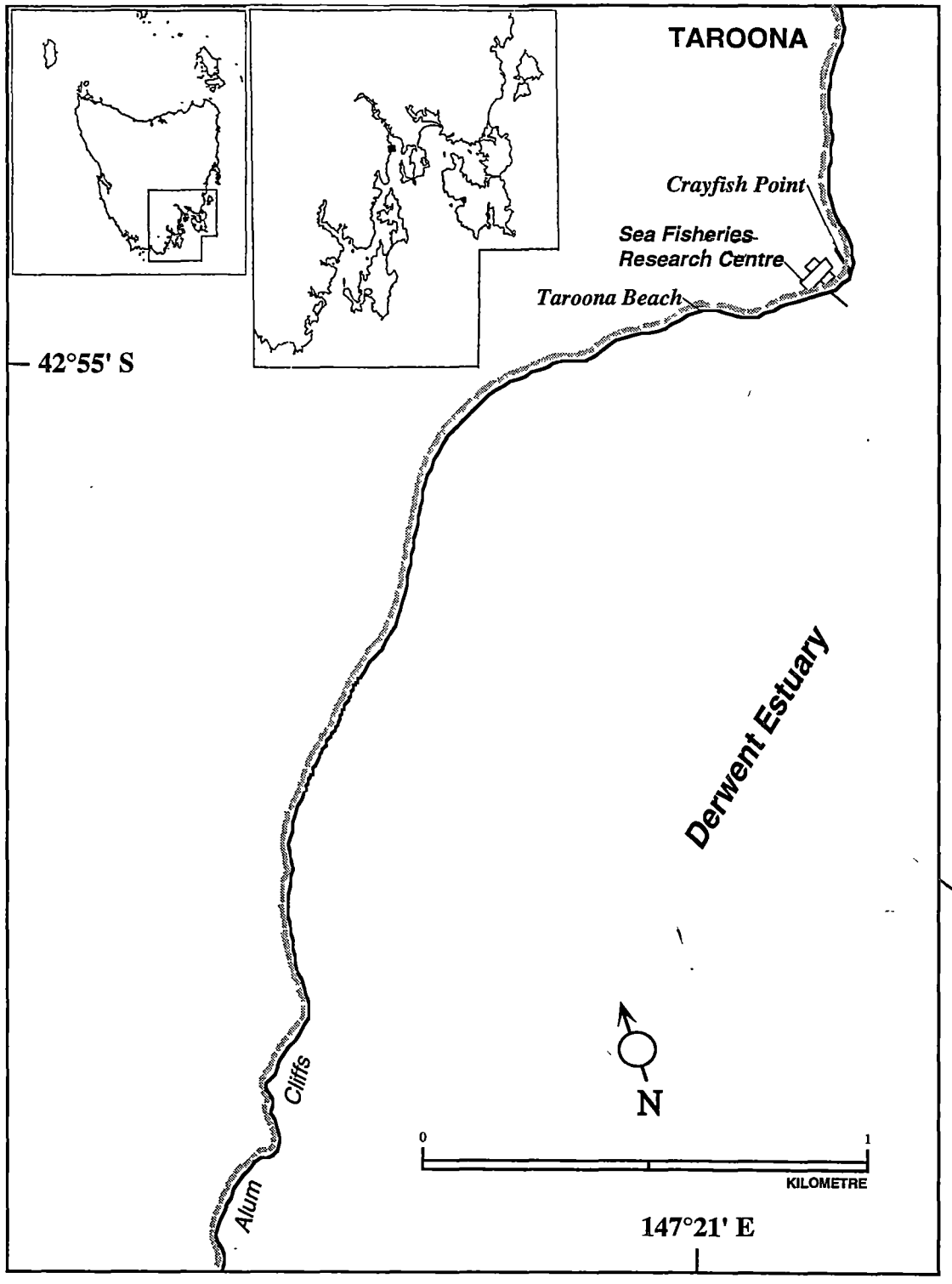


Figure 5.1 Map showing site of mysid collection and *in situ* feeding studies.
Inset: maps of Tasmania and southeast Tasmania (black square - study site).

Late Spring and Early Autumn Experiments (Mysid Species Held Separately)

Both field and laboratory methods used are essentially similar to those outlined by Mullin and Roman (1986).

Preparation of Foodstuff

Three types of food were offered to the three mysid species:

(1) algal detritus prepared from *Lessonia corrugata* (a brown alga, dominant in the study site). After 2 days oven drying at 60°C, the alga was ground and sieved through a 63 μm mesh net. Radiolabelling was done by suspending 620 mg of < 63 μm algal particles in 500 ml sterile seawater, keeping the suspension in the dark at 12-15 °C for three days to allow growth of attached bacteria, and allowing bacteria to incorporate [methyl-^{3}H]-thymidine (3 μCi mL^{-1}) as they multiplied. Labelling was completed 2 days before the field experiment. Labelled algal detritus were filtered onto 0.8 μm Whatman membrane filter and thrice resuspended in sterile filtered seawater;

(2) The phytoflagellate *Isochrysis galbana* (CSIRO Culture Collection). *I. galbana* was grown in f2 medium under 12h light:12h dark photoperiod (CSIRO Algal Culture Laboratory). Two-day radiolabelling of log-phase cells was by photosynthetic uptake of $NaH^{14}CO_3$ (5 μCi mL^{-1}) under standard culture conditions recommended by CSIRO; and

(3) Four-day old nauplii of *Artemia* sp. Mature cysts (Artemia Revolution®, New Technology, Kent, England) were hatched in the laboratory following similar procedures as in chapter 4. Two days before the field experiment, two-day old nauplii were allowed to graze on ^{14}C-labelled *I. galbana*. Radioactively labelled nauplii were thrice washed in sterile filtered seawater.

Table 5.1 Radiofeeding experiment with three mysid species: field conditions, initial food concentration, number of mysids.

	Experiment Number	
	I	II
Date:	23 November 1992	11 March 1993
Salinity (‰):	34	35
Temperature (°C):	15	16
Depth (m)	2 - 3	2 - 3
Location:	Off Sea Fisheries Bldg., Taroona	Off Taroona Beach
Turbulence:	low to medium	low
Duration:	1030h - 1455h	1030h - 1345h
Tide:	low	low
Predicted tide data*:	time height (m)	time height (m)
	0619 1.85	0503 0.70
	1400 0.67	1214 0.72
	2023 1.38	1753 0.99
	2358 1.30	2305 1.70
Food Concentration ($\mu gC \cdot mL^{-1}$):		
Algal Detritus (*Lessonia corrugata*)	0.105	0.105
Zooplankton (*Artemia* sp.)	0.200	0.160
Phytoplankton (*Isochrysis galbana*)	0.104	0.080
Mysid Number (Biomass (mg DW)):		
Chamber 1		
a. *Paramesopodopsis rufa*	57 (70.4)	188 (166.0)
a. *Tenagomysis tasmaniae*	42 (26.7)	242 (126.2)
a. *Anisomysis mixta australis*	---	452 (89.6)
Chamber 2		
b. *Paramesopodopsis rufa*	43 (63.3)	106 (193.9)
b. *Tenagomysis tasmaniae*	33 (18.0)	58 (23.7)
b. *Anisomysis mixta australis*	---	662 (165.1)
Chamber 3		
c. *Paramesopodopsis rufa*	19 (34.1)	43 (78.3)
c. *Tenagomysis tasmaniae*	65 (44.1)	48 (25.0)
c. *Anisomysis mixta australis*	---	49 (12.2)

* Tasmania Tide Tables, Issued by Port Authorities, Marine Board of Hobart

Experiments No. I and II
a,b, c = replicates

Experiment No. III
a,b - replicate 1 (algal detritus and zooplankton mixture)
c,d - replicate 2 (algal detritus and zooplankton mixture)
e,f - replicate 1 (algal detritus and phytoplankton mixture)
g,h - replicate 2 (algal detritus and phytoplankton mixture)

Experiment No. IV
a,b - replicate for algal detritus and zooplankton mixture
c,d - replicate for algal detritus and phytoplankton mixture

Table 5.1 continuation.

	Experiment Number III		Experiment Number IV	
Date:	5 April 1994		29 July 1994	
Salinity (‰):	34		33	
Temperature (°C):	15		8.5	
Depth (m)	1.5 - 2		2 - 2.5	
Location:	Off Taroona Beach		Off Taroona Beach	
Turbulence:	low to medium		medium to high	
Duration:	1130h - 1615h		1020h - 1145h	
Tide:	low			
Predicted tide data*:	time	height (m)	time	height (m)
	0330	1.64	0054	1.45
	1036	0.77	0704	1.12
	1715	1.48	1338	1.68
	2231	1.15	2030	1.14
Food Concentration ($\mu gC \cdot mL^{-1}$):				
Algal Detritus (*Lessonia corrugata*)	1.010		0.920	
Zooplankton (*Artemia* sp.)	0.444		0.376	
Phytoplankton (*Isochrysis galbana*)	0.212		8.090 (*Scrippsiella trochoidea*)	
Mysid Number (Biomass (mg DW)):				
Chamber 1			Chamber 1	
a. *P. rufa*	47 (9.4)		a. *A. mixta australis*	51 (19.4)
b. *A. mixta australis*	21 (26.7)		b. *T. tasmaniae*	24 (22.1)
c. *P. rufa*	55 (18.9)		c. *A. mixta australis*	61 (22.2)
d. *A. mixta australis*	41 (11.2)		d. *P. rufa*	44 (74.5)
e. *P. rufa*	47 (80.4)		Chamber 2	
f. *A. mixta australis*	32 (9.7)		a. *A. mixta australis*	63 (23.1)
g. *P. rufa*	83 (145.4)		b. *P. rufa*	42 (86.9)
h. *A. mixta australis*	60 (16.4)		c. *A. mixta australis*	60 (21.5)
Chamber 2			d. *P. rufa*	42 (73.2)
a. *A. mixta australis*	12 (10.6)		Chamber 3	
b. *T. tasmaniae*	33 (18.02)		a. *A. mixta australis*	54 (19.6)
c. *A. mixta australis*	40 (14.0)		b. *P. rufa*	45 (87.8)
d. *T. tasmaniae*	48 (45.7)		c. *A. mixta australis*	43 (15.5)
e. *A. mixta australis*	54 (17.6)		d. *P. rufa*	46 (106.9)
f. *T. tasmaniae*	46 (39.0)			
g. *A. mixta australis*	58 (14.3)			
h. *T. tasmaniae*	87 (74.3)			
Chamber 3				
a. *P. rufa*	49 (99.9)			
b. *T. tasmaniae*	54 (48.9)			
c. *P. rufa*	50 (93.6)			
d. *T. tasmaniae*	42 (36.6)			
e. *P. rufa*	50 (84.7)			
f. *T. tasmaniae*	46 (40.1)			
g. *P. rufa*	94 (156.4)			
h. *T. tasmaniae*	91 (78.5)			

Feeding Chamber

A modified Mullin (1983) 5-L (inner diameter = 14.4 cm) clear perspex cylinder was used as the feeding chamber (Fig. 5.2). The chamber bears a screw cap on one end and a 1 mm thick rubber diaphragm at the opposite end. A plastic tubing entry port for the radiolabelled food is situated on the plastic plate where the diaphragm is attached.

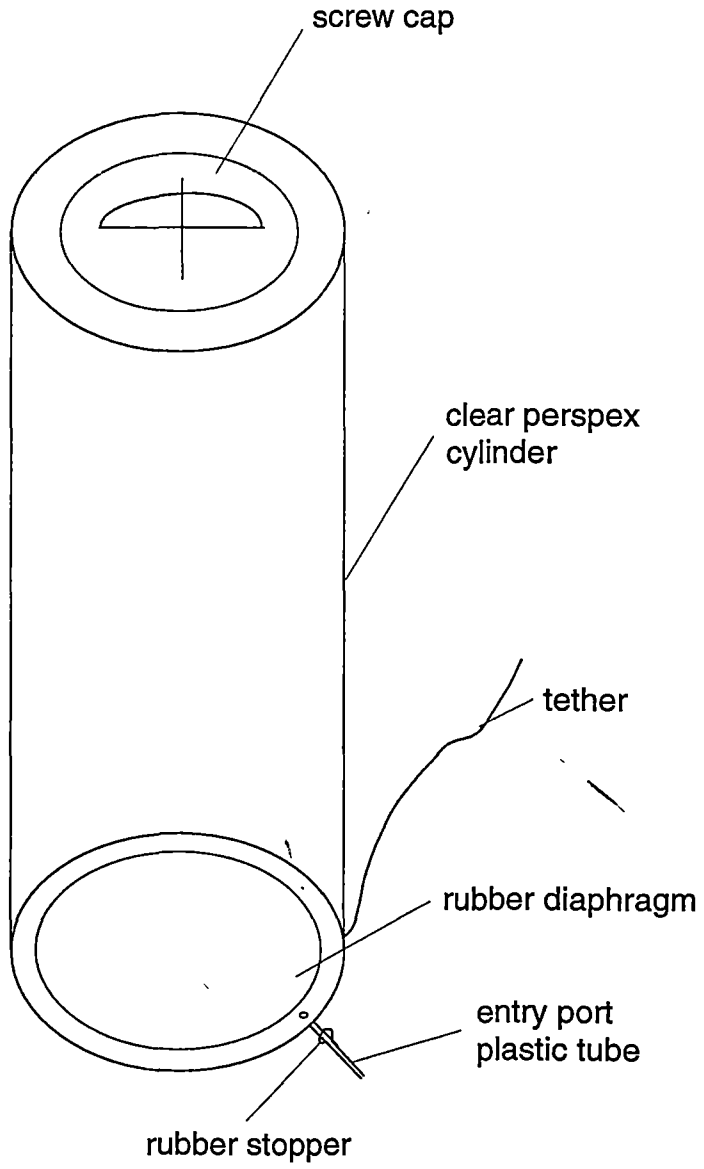


Figure 5.2 The grazing chamber used in the *in situ* experiments. Not to scale.

"Field" Methods

Two series of experiments were conducted, one in late spring (23 November 1992) and one in early autumn (16 March 1993). Two SCUBA divers carried out the experiment between 1000-1450 h (see Table 5.1); one of them tied three chambers to weights placed adjacent to the area where the other diver caught the animals. Mysids were placed in each chamber, and were allowed to acclimatize for 20 to 30 min during which they resumed aggregating inside the chamber. Fifty mL of each of the ^{3}H- and ^{14}C-labelled food suspension were injected into a chamber: chambers 1 and 3 were injected with phytoplankton and algal detritus, and chamber 2 was injected with zooplankton and algal detritus. To determine levels of adsorbed radioactive labels, chamber 3 served as control which was further injected with buffered formalin (3-5% final concentration) to rapidly kill the mysids. Contents of the chamber were mixed by re-injecting the contents of the syringe twice. Prior tests using a dye showed that this method resulted in efficient mixing of the chamber contents. A 50-mL sample was withdrawn for initial food radioactivity determination from the control and treatment chambers. The samples were immediately filtered through 0.45 µm (pore size) HA Millipore filters (2.5 cm diameter). Filters were placed in glass scintillation vials and stored in ice-filled eski containers. Gut residence time of food is highly variable in mysids (Murtaugh 1984), and in the present study, mysids were allowed 20-min feeding time which was assumed to be shorter than their food gut passage time. In this manner, recycling of isotopes and underestimates of radioactivity due to excretion were avoided. Soon after incubation another 50-ml sample was withdrawn from the chambers for final food radioactivity determination, filtered immediately, and filters treated as in the initial samples. Feeding chambers were drained through a 1 mm mesh and trapped mysids were immediately killed in hot distilled water. Groups of 20-30 mysids on Millipore filters were placed in scintillation vials which were then stored with the other filters. *Artemia* sp nauplii were separated from other seston by re-filtering the contents of the chamber through 250 µm mesh.

Laboratory Methods

Measuring Radioactivity in Samples

Prior to crushing with a clean glass rod in their scintillation vials, mysid lengths from anterior tip of carapace rostrum-to-tip of telson were measured using a vernier caliper. Five to seven drops of hydrogen peroxide were added to bleach specimens for 15 min. Samples (mysids, food) were dissolved in 1 mL Soluene (solubilizing fluid from Packard Instruments International, Zurich, Switzerland) at 50-55 °C. To each cooled sample, 10 mL glacial acetic acid was added and mixed prior to the addition of 4 mL Opti-Fluor (scintillation fluid from Packard Instruments International, Zurich, Switzerland). Samples were kept in darkness for 2 days. Sample radioactivity in disintegrations per minute (dpm) was measured in a liquid scintillation counter (Beckman Instruments, Inc., USA), adjusted to count ^{3}H and ^{14}C quenched series. The radioactivity for the food suspension was obtained from the geometric mean of initial and final samples.

Determination of Grazing and Ingestion Rates

Grazing or clearance rate was calculated using the formula of Mullin and Roman (1986):

$$GR = \frac{\text{dpm/mg DW mysid}}{\text{dpm/(mL of food suspension x h of incubation)}},$$

while ingestion rate (IR in µgC [mgDW mysid]$^{-1}$ h^{-1}) was calculated by multiplying grazing rate by the initial food concentration in µgC mL^{-1}. Since this study compares three mysid species, in order to remove the bias due to size differences, GR and IR are expressed in terms of mysid biomass (mgDW) rather than number. Mysid dry weight determinations follow the procedures of Fenton (1986). Mysid grazing rates on algal detritus were corrected for algal detritus grazed by *Artemia* sp. (see Appendix 1,2). Food and mysid dry weight data were converted to carbon values to estimate amount of food ingested in terms of mysid bodily carbon. Carbon determinations of both mysid and algal detritus were performed using a Carlo-Erba nutrient analyser. Carbon

values for *Artemia* sp. nauplii, *Isochrysis galbana*, and *Scrippsiella trochoidea* Stein were obtained from Omori and Ikeda (1984).

Measuring Selectivity Coefficients

Selectivity (S) for a certain food type in a double choice situation was calculated using the index by Lampert (1974, cited in Roman and Rublee 1981):

$$S = \frac{^{14}C \text{ (suspension) X } ^{3}H \text{ (animal)}}{^{3}H \text{ (suspension) X } ^{14}C \text{ (animal)}}$$

Mysids fed non-selectively if S=1, selection was for algal detritus if S > 1, and selection for the alternative food type if S < 1.

Mid-Autumn and Mid-Winter Experiments (Mysid Species Held Together)

Two series of experiments were undertaken, one in mid-autumn (5 April 1994) and another in mid-winter (29 July 1994), to investigate the effect of two of the three mysid species held together in a chamber on the feeding rates of each species. In the mid-autumn experiment, each of the three possible combinations, *A. m. australis* and *P. rufa*, *A. m. australis* and *T. tasmaniae*, and *P. rufa* and *T. tasmaniae*, was assigned to a grazing chamber. Mysids were collected the day before the experiment for a 12-h starvation period. Fifty individuals of each species were carefully transferred using a wide-bore pipette into 2-L plastic bags containing 5 µm Omni-Basic®-filtered and UV-treated ambient seawater. In this experiment, animals were placed in the grazing chambers before they were brought underwater. We had to adopt this change because the underwater transfer of the animals into the chamber as done in the earlier experiments was so time consuming. By doing this, the experiment finished within the same duration as in the previous experiments despite the increased number of chambers dictated by the experimental design. These modified procedures did not affect the behaviour of mysids as they resumed schooling inside the chamber after 10-12 min.

The food combinations of either ^{3}H-thymidine-labelled algal detritus and ^{14}C-labelled *Artemia* sp. metanauplii or ^{3}H-thymidine-labelled algal detritus and ^{14}C-labelled *Isochrysis galbana* were injected into a grazing chamber. The amount of algal detritus was increased by an order of magnitude, and those for the other food types were increased two-fold compared to the first two experiments (Table 6.1). Each experimental unit which comprised a pair of mysid species feeding on a mixture of two food types was replicated twice. The rest of the field and laboratory procedures were similar to the previous experiments.

The few *T. tasmaniae* caught the day before the mid-winter experiment permitted us to perform only one replicate for the *T. tasmaniae* and *A. mixta australis* combination fed with algal detritus and zooplankton mixture. More than enough of the other two species were caught, thus allowing two replications for the *A. mixta australis* and *P. rufa* combination. The phytoplankton food in the mid-winter experiment was changed to a larger sized dinoflagellate species (*Scrippsiella trochoidea* Stein) because in the first two and in the mid-autumn experiments, the three mysid species consistently poorly ingested the small sized *Isochrysis galbana*. *S. trochoidea* was grown following the same procedure as that for *I. galbana*. *S. trochoidea* cells in their log phase of growth were used in the feeding experiment. The concentration of *S. trochoidea* in the grazing chamber was 6,377 cells ml^{-1}, which is equivalent to 8.09 $\mu gC\ mL^{-1}$, forty times higher than the amount of *I. galbana*. used in the previous experiments (Table 6.1). The amounts of algal detritus and *Artemia* sp. nauplii used in the mid-winter experiment were comparable to those in the mid-autumn experiment (Table 6.1). The rest of the field and laboratory procedures were similar to the mid-autumn experiment.

Suspended particulate organic carbon (POC) in "field" seawater was analyzed only during these two series of experiments. Seawater was sampled during the *in situ* experiment using 2-L unused plastic jars with screw cap. Samples were frozen prior to the analysis of POC. The wet oxidation method (Parsons *et al.* 1984a) was used to determine POC.

Data Analysis

Non-parametric statistical tests were used in the present study because of the huge variability usually associated with suspension feeding rates (Paffenhøffer 1988). The Kruskal-Wallis test was used for the analysis of variance, and the Mann-Whitney *U*-test for comparing significant difference ($\alpha = 0.05$) between two arithmetic means.

Results

Total Length-Biomass (mgDW, µgC) Relationships

The following are the regression equations of the line of best fit for total length (mm) vs dry weight (mg) and total length (mm) vs body carbon (µg) for the three mysid species:

Anisomysis mixta australis

1. log dry weight = 2.89 (log total length) - 2.54 ($r^2 = 0.962$, $F = 23.14$, df = 1, $p < 0.0001$)

2. log body carbon = 2.71 (log total length) + 0.197 ($r^2 = 0.996$, $F = 43680.70$, df = 1, $p < 0.0001$)

Paramesopodopsis rufa

1. log dry weight = 2.96 (log total length) - 2.52 ($r^2 = 0.960$, $F = 31.41$, df = 1, $p < 0.0001$)

2. log body carbon = 2.94 (log total length) + 0.087 ($r^2 = 0.995$, $F = 69528.37$, df = 1, $p < 0.0001$)

Tenagomysis tasmaniae

1. log dry weight = 2.50 (log total length) - 2.24 ($r^2 = 0.987$, $F = 6.51$, df = 1, $p < 0.05$)

2. log body carbon = 2.48 (log total length) + 0.373 ($r^2 = 0.989$, $F = 4936.45$, df = 1, $p < 0.0001$)

Mysid Species Held Separately

Feeding Rates

Results from the late spring and early autumn experiments (conditions shown in Table 5.1) are shown in Figures 5.3A,B to 5.4A,B. Data are presented as mysid clearance rate per feeding chamber because values obtained varied widely. Formalin preserved mysids from control chambers showed dpm levels less than 10% of those from the experimental chambers which is similar to results reported by Roman and Rublee (1981). A very wide range of GR values from grazing chambers resulted in no significant difference between mysid species grazing upon algal detritus ($H = 1.93$, df = 2, $p > 0.05$), *Isochrysis galbana* ($H = 3$, df =2, $p > 0.05$), and zooplankton ($H = 0.473$, df =2, $p > 0.05$). Pooling all data from the three species for a particular food type resulted in similar clearance rates for the different food types by all three mysid species ($H = 1.28$, df = 2, $p > 0.05$).

Paramesopodopsis rufa showed a relatively higher range of clearance rates of the different foodstuffs offered compared to the other two mysid species. In the first experiment, clearance rate of 41 mL $mgDW^{-1}$ h^{-1} (single value) on phytoplankton and an average of 25.67 (± 12.88 SE) on algal detritus indicate that *P. rufa* ingested more of these food types than zooplankton with average clearance rate of 11 mL $mgDW^{-1}$ h^{-1} (± 5 SE). However, in experiment 2 the reverse happened in that more nauplii of *Artemia* sp. were eaten with a clearance rate of 84 mL $mgDW^{-1}$ h^{-1} than phytoplankton (GR = 2) and algal detritus (average GR = 2.5 ± 1.5 SE). *Paramesopodopsis rufa* ingested an equivalent of 1-2 nauplii $mgDW^{-1}$ h^{-1} in the first experiment and up to 8 nauplii in the second.

In both experiments, *T. tasmaniae* showed comparable clearance rates to those of *A. mixta australis*. *T. tasmaniae* showed slightly higher clearance rates on algal detritus with an average of 5 mL $mgDW^{-1}$ h^{-1} (± 1.53 SE) than on phytoplankton which averaged 3 mL $mgDW^{-1}$ h^{-1} (± 2 SE). In the first experiment, a clearance rate on zooplankton of 1.2 mL $mgDW^{-1}$ h^{-1} suggests very few individual *T. tasmaniae* in the chamber ingested zooplankton. The value is equivalent to ingesting only 0.13 of

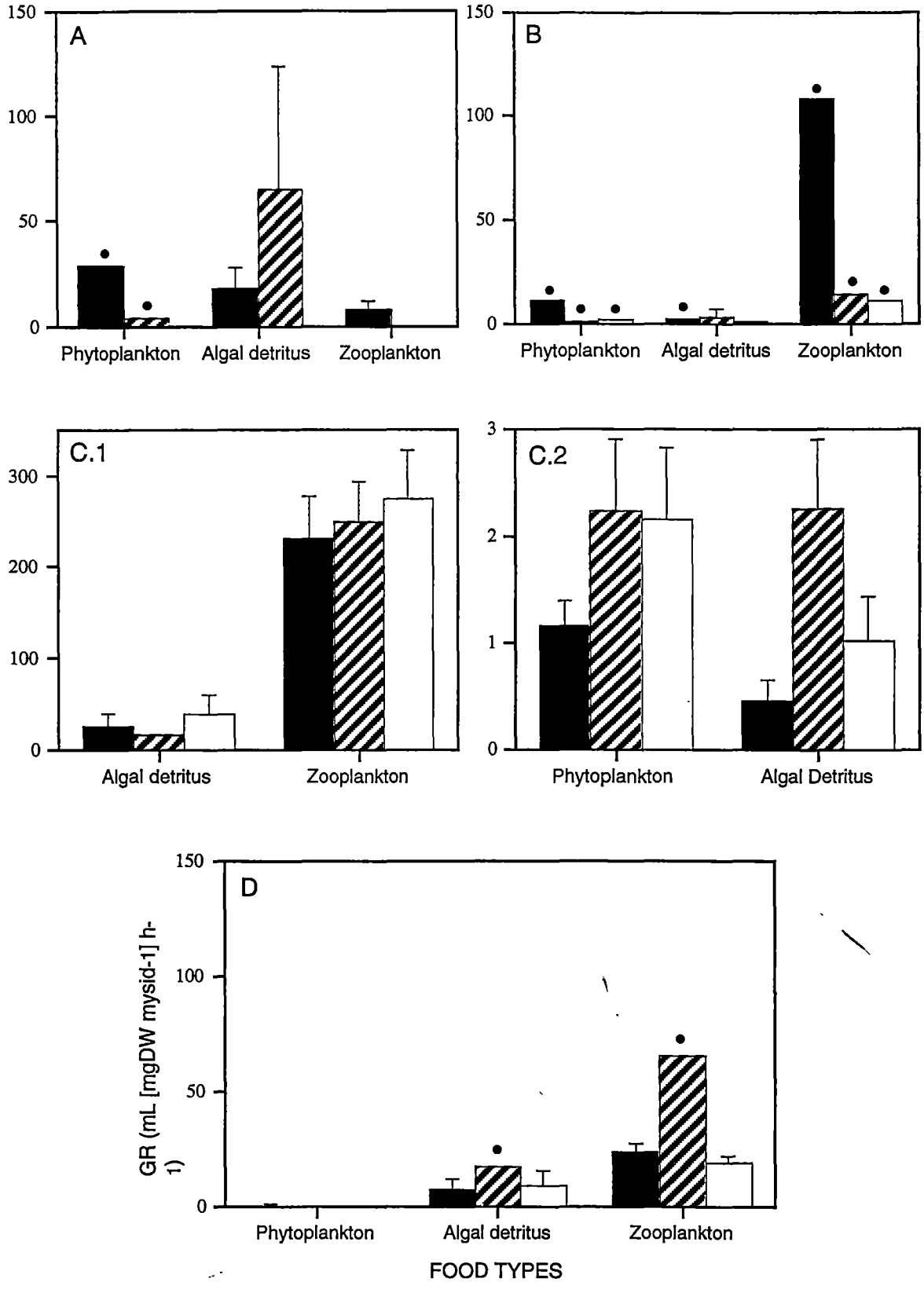


Figure 5.3 Grazing rates (GR) of three radioisotope labelled food types by three co-occurring mysid species. A-D. Data from experiments I-IV. Food types: phytoplankton - *Isochrysis galbana* (experiments I-III), *Scrippsiella trochoidea* (experiment IV); algal detritus - *Lessonia corrugata*; zooplankton - *Artemia* sp. metanauplii. Solid bars - *Paramesopdopsis rufa*, hatched bars - *Tenagomysis tasmaniae*, open bars - *Anisomysis mixta australis*. Titles for x and y axes in A-C are identical to those in D. • - single value. Error bars: standard error.

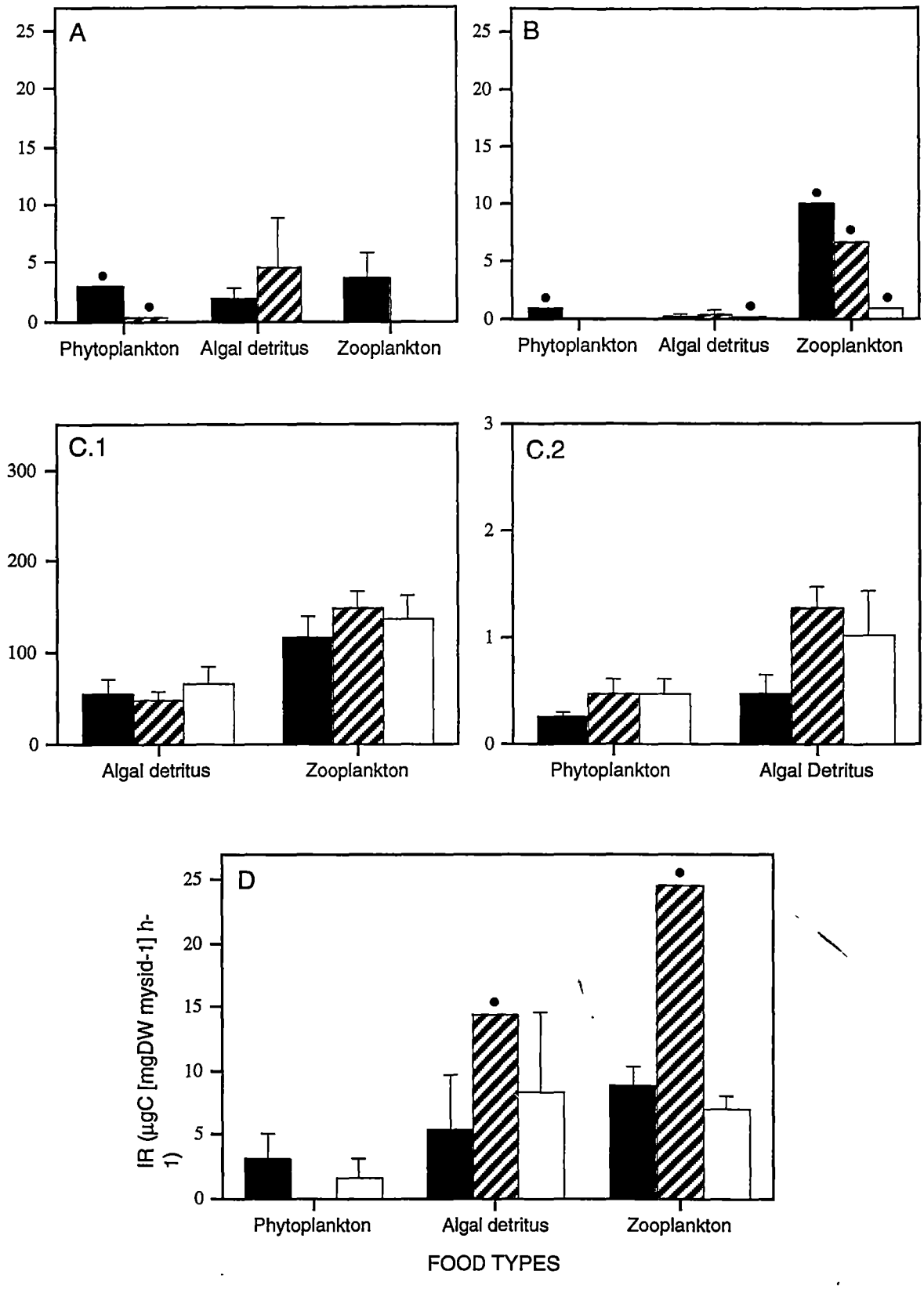


Figure 5.4 Ingestion rates (IR) of three radioisotope labelled food types by three co-occurring mysid species. A-D. Data from experiments I-IV. Food types: phytoplankton - *Isochrysis galbana* (experiments I-III), *Scrippsiella trochoidea* (experiment IV); algal detritus - *Lessonia corrugata*; zooplankton - *Artemia* sp. metanauplii. Solid bars - *Paramesopdopsis rufa*, hatched bars - *Tenagomysis tasmaniae*, open bars - *Anisomysis mixta australis*. Titles for x and y axes in A-C are identical to those in D. • - single value. Error bars: standard error.

an individual *Artemia* nauplius mgDW^{-1} h^{-1} for *T. tasmaniae*. However, in the second experiment *T. tasmaniae* showed a clearance rate of 11 mL mgDW^{-1} h^{-1} which is equivalent to ingesting 1 nauplius mgDW^{-1} h^{-1}.

Data on *A. mixta australis* were only from the second experiment because this species was not captured on the first occasion. *Anisomysis mixta australis* showed higher average clearance rate of 4.5 mL mgDW^{-1} h^{-1} (± 1.5 SE) on algal detritus than on phytoplankton, with a clearance rate of 1 mL mgDW^{-1} h^{-1}. The slightly higher clearance rate of 8 mL mgDW^{-1} h^{-1} on zooplankton than the other food types suggests very few *A. m. australis* ingested the animal prey. The clearance rate on zooplankton is equivalent to ingesting 0.8 of one *Artemia* nauplii mgDW^{-1} h^{-1}.

Ingestion rates showed no significant difference between mysid species ingesting algal detritus (H = 1.92, df = 2, $p > 0.05$), *Isochrysis galbana* (H = 3, df = 2, $p > 0.05$), and zooplankton (H = 2.29, df =2, $p > 0.05$). However, pooled ingestion rate data from the three species for a particular food type revealed that all three species ingested more *Artemia* sp. nauplii than the other two food types offerred (H = 7.18, df = 2, $p < 0.05$). Ingestion rates of algal detritus by *P. rufa* ranged from 0.23 to 3.76 µgC mgDW^{-1} h^{-1} while those of *T. tasmaniae* ranged from 0.02-12.96. *A. m. australis* had only one value of 0.5 µgC mgDW^{-1} h^{-1}. *P. rufa* ingested *I. galbana* cells from 0.12-2.96 µgC mgDW^{-1} h^{-1}. The other two species had only single values with *T. tasmaniae* ingesting *I. galbana* cells at 0.06 µgC mgDW^{-1} h^{-1} and *A. mixta australis* at 0.37. *Paramesopodopsis rufa* consumed *Artemia* sp. nauplii in a ranged 1.39-9.91 µgC mgDW^{-1} h^{-1}, and the equivalent values by *T. tasmaniae* were from 1.11 to 7.13. The single ingestion rate value by *A. m. australis* was 10.61 µgC nauplii mgDW^{-1} h^{-1}.

Paramesopodopsis rufa showed a wide range of values for the percent body carbon ingested per hour, and overall these were generally higher than in the other two species. Ingested phytoplankton accounted for 0.1-0.8% of mysid body carbon h^{-1}. Hourly ingested algal detritus was equivalent to 0.2-1% of *P. rufa*'s bodily carbon. *Paramesopodopsis rufa* ingested 0.2-6.1% of its bodily carbon h^{-1} when feeding on the nauplii of *Artemia* sp. On the other hand, *T. tasmaniae* ingested 0.1-0.2% of its

bodily carbon h^{-1} on phytoplankton, 0.1-0.4% on algal detritus, and 1.13% on *Artemia* sp. nauplii. Half of the minimum value achieved by the two larger species was shown in *A. mixta australis* with 0.5% of its bodily carbon h^{-1} from ingesting phytoplankton. *A. mixta australis* consumed comparable proportions of bodily carbon per hour as *T. tasmaniae* (0.2-0.4%) feeding on algal detritus. Ingestion of the live animal prey was at a rate of 0.7% of *A. mixta australis* bodily carbon per hour.

Selectivity Coefficients

Table 5.2 shows selectivity coefficients of the three mysid species for the different food types offered in experiments I and II. *P. rufa* fed non-selectively on phytoplankton and algal detritus in both experiments 1 and 2. In experiment I, selection for algal detritus was shown which contrasts with the preference for zooplankton in experiment II. In all food choices in experiment I, a preference for algal detritus was shown by *T. tasmaniae*, but it became non-selective between phytoplankton and algal detritus and preferred zooplankton in experiment II. In experiment II, selection for algal detritus and zooplankton was apparent in *A. mixta australis*.

Table 5.2 Feeding selectivity (S) in three co-occurring mysid species held separately. S = 1, non selective feeding; S > 1, selection for algal detritus; S < 1, selection for the alternative food.

	Paramesopodopsis rufa		*Tenagomysis tasmaniae*		*Anisomysis mixta australis*	
	Experiment No.		Experiment No.		Experiment No.	
Food Types	I	II	I	II	I	II
phytoplankton VS algal detritus	1.20	1.06	1.47	1.09	—	5.50
zooplankton VS algal detritus	1.55, 1.04	0.06	2.06	0.44	—	0.50

Feeding Rates in the Mid-Autumn Experiment

Clearance rates by the three species feeding on algal detritus paired with the *Artemia* sp. nauplii were an order of magnitude higher than those for phytoplankton-algal detritus pair ($H = 20.48$, df = 2, $p < 0.001$) (Figure 5.3C.1). The average grazing rates by all three species for this food were comparable ($H = 1.12$, df = 2, $p > 0.05$) with 15.28 (± 0.70 SE) mL mgDW^{-1} h^{-1} for *T. tasmaniae*, 23.79 (± 14.20 SE) for *P. rufa*, and 38.97 (± 18.99 SE) for *A. mixta australis*. Average grazing rates on *Artemia* sp. nauplii ranged from 229.68 (*P. rufa*) to 274.99 (*A. mixta australis*) mL mgDW^{-1} h^{-1} and were similar for all three species ($H = 0.15$, df = 2, $p >> 0.05$), but an order of magnitude higher than those in either algal detritus mixed with *Artemia* or phytoplankton-algal detritus mixture ($H = 36.52$, df = 3, $p < 0.001$). The three mysid species' comparable clearance rates ($H = 4.27$, df = 2, $p >> 0.05$) were lowest for the algal detritus mixed with *Isochrysis gabana* (Figure 5.3C.2). Average clearance rates ranged from 0.45 (*P. rufa*)-1.26 (*T. tasmaniae*) mL mgDW^{-1} h^{-1}. Average clearance rates in all three mysid species feeding on *I. galbana* were similar ($H = 1.85$, df = 2, $p >> 0.05$), but greater than those for algal detritus ($U = 112$, df = 1, $p < 0.05$). The three species grazed *I. galbana* cells at averages ranging from 1.15 (*P. rufa*) to 2.23 (*T. tasmaniae*) mL mgDW^{-1} h^{-1}.

The three species' ingestion rates for algal detritus paired with *Artemia* sp. nauplii were similar ($H = 0.67$, df = 2, $p >> 0.05$), but an order of magnitude higher than those for both algal detritus mixed with *Isochrysis* sp ($H = 20.27$, df = 2, $p < 0.001$) (Figure 5.4C1). Average ingestion rates ranged from 48.48 (*T. tasmaniae*) to 66.06 (*A. mixta australis*) µgC of algal detritus mgDW^{-1} h^{-1}. Average ingestion rates of the *Artemia* sp. nauplii were an order of magnitude higher ($H = 36.06$, df = 3, $p < 0.001$), and ranged from 116.34 (*P. rufa*) to 149.15 (*T. tasmaniae*) µgC of nauplii mgDW^{-1} h^{-1}. Rates of ingestion of algal detritus by the three mysid species were higher than those for *I. galbana* ($U = 33.50$, df = 1, $p < 0.05$) (Figure 5.4C2). However, for each food type, all three species showed comparable rates (for both

food types, $H > 1.85$, df = 2, $p >> 0.05$). Average ingestion rates ranged from 0.46 (*P. rufa*) to 1.27 (*T. tasmaniae*) µgC algal detritus mgDW^{-1} h^{-1}, and 0.46 (*A. mixta australis*) to 0.47 (*T. tasmaniae*) µgC *I. galbana* mgDW^{-1} h^{-1}.

The feeding rates on *I. galbana* in terms of body carbon hr^{-1} were equivalent to an average of 0.07 % (0.01 SE) for *P. rufa*'s bodily carbon h^{-1}, 0.11% (± 0.03 SE) for *A. mixta australis*, and 0.12 % (± 0.03 SE) for *T. tasmaniae*. These values were not significantly different ($H = 1.24$, df = 2, $p > 0.05$), and were lower than those for the algal detritus paired with *I. galbana* ($U = 33$, df = 2, $p < 0.05$). The feeding rates (body carbon h^{-1}) of the three mysid species for this algal detritus were similar ($H =$ 4.27, df = 2, $p >> 0.05$) with *P. rufa* ingesting this food type at an average of 0.12 % (± 0.05 SE), *A. mixta australis* at an average of 0.25 % (± 0.10 SE), and *T. tasmaniae* at average of 0.32 % (± 0.05 SE). The feeding rates (body carbon h^{-1}) on algal detritus paired with *Artemia* sp. nauplii were equivalent to ingesting 12.20 % (± 1.94 SE) for *T. tasmaniae*, 16.08 % (± 4.44 SE) for *A. mixta australis*, and 13.53 % (± 4.00 SE) for *P. rufa*. These values are similar ($H = 0.46$, df = 2, $p >> 0.05$.), and an order of magnitude higher than those for consumption of *I. galbana* and its algal detritus pair ($H = 20.35$, df = 2, $p < 0.001$). The feeding rates on *Artemia* sp. nauplii by the three species (body carbon h^{-1}) were equivalent to feeding 53.73 % (± 11.02 SE) of *P. rufa*, 57.78 % (± 10.14 SE) of *T. tasmaniae*, and 71.62 % (± 14.15 SE) of *A. mixta australis*. These values are not significantly different from each other ($H =$ 1.08, df = 2, $p >> 0.05$), but are two orders of magnitude higher than those for consumption of *I. galbana* and its pair algal detritus, and 5 to 6 times greater than those for algal detritus paired with *Artemia* sp. nauplii ($H = 36.46$, df = 3, $p < 0.001$).

Mid-Winter Experiment

Comparable clearance rates for *Artemia* sp. nauplii were achieved by the three mysid species ($H = 3.14$, df = 2, $p > 0.05$) (Figure 5.3D). The average clearance rates by *A. mixta australis* was 18.94 (± 2.40 SE) mL mgDW mysid^{-1} h^{-1}, and that in *P. rufa* was 23.48. Only one value was obtained for *T. tasmaniae*, *i.e.* 65.28 mL mgDW^{-1} h^{-1}. These values are similar to those for the algal detritus mixed with the

nauplii (H = 11. df = 2, $p > 0.05$). This particular algal detritus was cleared by the three mysid species at comparable rates (H =0.43, df = 2, $p > 0.05$), *i.e.* an average of 16.21 (± 12.86 SE) mL mgDW^{-1} h^{-1} for *A. mixta australis*, *P. rufa* at an average of 11.65 (± 6.59 SE) mL mgDW^{-1} h^{-1}, and a single value of 16.97 mL mgDW^{-1} h^{-1} for *T. tasmaniae*. Both clearance rates for *Artemia* sp. nauplii and its pair algal detritus were one to two orders of magnitude higher than those for the algal detritus mixed with *Scripssiella trochoidea*, and for *S. trochoidea* itself (H = 14.85, df = 3, $p <$ 0.05). The average clearance rate by *A. mixta australis* for the algal detritus paired with *S. trochoidea* was 1.24 (± 0.06 SE) mL mgDW^{-1} h^{-1}, and that for *P. rufa* was 1.06 (± 0.34 SE). The average clearance rate of *A. mixta australis* for *S. trochoidea* was 0.19 (± 0.18 SE) mL mgDW^{-1} h^{-1}, and that of *P. rufa* was 0.38 (± 0.25 SE). Clearance rates by the three species for both algal detritus and its pair *S. trochoidea* were comparable (U = 2, df = 1, $p >> 0.05$)

Ingestion rates by *A. mixta australis* and *P. rufa* feeding on *S. trochoidea* were comparable to those for its algal detritus pair (U = 9, df =1, $p > 0.05$) (Figure 5.4D). *A. mixta australis* ingested an average of 1.56 (± 1.46 SE) µgC *S. trochoidea* mgDW^{-1} h^{-1}, and an average of 1.14 (± 0.05) µgC algal detritus mgDW^{-1} h^{-1}. The average ingestion rates by *P. rufa* were 3.02 (± 2.08 SE) µgC *S. trochoidea* mgDW^{-1} h^{-1}, and 0.86 (± 0.20 SE) µgC algal detritus mgDW^{-1} h^{-1}. *A. mixta australis* average hourly ingestion rates for this food type was 15.44 (± 11.71 SE) µgC mgDW^{-1}, that in *P. rufa* was at 8.32 (± 7.16 SE) µgC mgDW^{-1} h^{-1}, and the single value for *T. tasmaniae* was 17.47 µgC mgDW^{-1} h^{-1}. These rates are comparable to the ingestion rates of *Artemia* sp. nauplii by the three species (U = 21, df =1, $p >>0.05$). *T. tasmaniae* ingested 24.55 µgC *Artemia* sp. nauplii mgDW^{-1} h^{-1} which was comparable to those in the other two species (H = 3.14, df = 2, $p > 0.05$). *A. mixta australis* average ingestion rate was 7.1 (± 0.89 SE) µgC of nauplii mgDW^{-1} h^{-1} while that of *P. rufa* was 8. 83 (± 1.54 SE) µgC of nauplii mgDW^{-1} h^{-1}. Ingestion rates by the three species feeding on *Artemia* sp nauplii and its algal detritus pair are one to two orders of magnitude higher than those for *S. trochoidea* and its pair algal detritus (H = 10.16, df =3, $p < 0.05$).

In terms of body carbon h^{-1} *A. mixta australis* ingested *S. trochoidea* at an average of 0.38 % (± 0.36 SE), and 0.28 % (± 0.007 SE) when it ingested the algal detritus mixed with *S. trochoidea*. Likewise, *P. rufa* ingested *S. trochoidea* at an average of 0.78 % (± 0.54 SE) of its bodily carbon h^{-1}, and algal detritus mixed with *S. trochoidea* at an average of 0.22 % (± 0.05 SE). The rates of the two species ingesting *S. trochoidea* were similar ($U = 1$, df =1, $p >> 0.05$), and were also comparable when they ingested the algal detritus mixed with *S. trochoidea* ($U = 3.5$, df = 1, $p > 0.05$). The equivalent hourly % bodily carbon ingestion of the algal detritus paired with *Artemia* sp. nauplii in the three species is similar to those for *S. trochoidea* and the algal detritus mixed with *S. trochoidea* ($H = 4.17$, df = 2, $p > 0.05$). In terms of body carbon h^{-1} *A. mixta australis* ingested algal detritus at an average of 3.81 % (± 2.9 SE), and 2.15 % (± 1.85 SE) for *P. rufa*, and the single value of 4.39 % for *T. tasmaniae*. The ingestion rates in terms of % bodily carbon h^{-1} of the three species ingesting algal detritus mixed with the nauplii are similar (Kruskal-Wallis test, $H = 1.24$, df = 2, $p > 0.05$). The rates in all three species for the nauplii alone are also comparable ($H = 3.14$, df = 2, $p > 0.05$). *T. tasmaniae* consumed *Artemia* sp. nauplii at 6.16 % of its bodily carbon h^{-1} (single value), *A. mixta australis* at an average of 1.74 % (± 0.21 SE), and *P. rufa* at an average of 2.29 % (± 0.40). The average hourly % bodily carbon ingestion by *A. mixta australis* and *P. rufa* feeding on *S. trochoidea* and its pair algal detritus are an order of magnitude lower than when the two species fed on *Artemia* sp. nauplii mixed with algal detritus ($H = 10.35$, df = 3, $p < 0.05$).

Particulate Organic Carbon in Seawater

The average POC in the mid-autumn experiment was 155.00 $\mu gC\ L^{-1}$ (± 6.52 SD, n = 2), while that in the mid-winter experiment was 369.73 $\mu gC\ L^{-1}$ (± 49.35 SD, n = 6). Suspended particulate macroalgae was abundant in during mid-winter.

Selectivity Coefficients

Selectivity coefficients by the three mysid species from both mid-autumn and

mid-winter experiments are shown in Table 5.3. *A. mixta australis* and *P. rufa* strongly selected algal detritus over phytoplankton in experiment IV, but all three species selected phytoplankton over algal detritus in experiment III. Zooplankton was strongly selected by all three species over algal detritus in experiments III and IV.

Table 5.3 Feeding selectivity (S ± standard error) in three co-occurring mysid species (species held together). S = 1, non selective feeding; S > 1, selection for algal detritus; S < 1, selection for the alternative food.

	Paramesopodopsis rufa		*Tenagomysis tasmaniae*		*Anisomysis mixta australis*	
	Experiment No.		Experiment No.		Experiment No.	
Food Types	III	IV	III	IV	III	IV
phytoplankton VS algal detritus	0.35 ± 0.09	5.50 ± 4.36	0.63 ± 0.22	---	0.36 ± 0.30	54.96 ± 51.78
zooplankton VS algal detritus	0.12 ± 0.02	0.14 ± 0.03	0.08 ± 0.02	0.06	0.09 ± 0.03	0.26 ± 0.11

Discussion

In the late spring and early autumn experiments (experiments I and II), very wide variation of grazing rates by the three mysid species on the three food types offered suggests no difference in feeding habits. However, the range of clearance rate values should indicate the extent to which a particular food type is grazed upon. For example, although *P. rufa* GR values for phytoplankton and algal detritus are not statistically different from those in the other two species, the fairly high clearance rate on zooplankton in experiment 2 suggests preference for that type of food. A probable effect of food interference is also apparent in *P. rufa*, as shown in the apparent switch of food preference between algal detritus and zooplankton. *T. tasmaniae* was always observed swimming very close to or lying on the bottom of the chamber during the experiment. This behaviour may influence availability and therefore clearance rates of food types offered, particularly of the *Artemia* sp. nauplii which remained swimming above the bottom. This suggests behavioural plasticity between mysid species and

that feeding rates are governed by these behavioural attributes as emphasized by Paffenhøffer (1988).

In the mid-autumn experiment, it is clearly demonstrated that holding two mysid species together in a chamber had no effect on the feeding rates on a particular food type by the three mysid species . Similar trends in the mid-winter experiment further support this conclusion. Perhaps in both experiments where feeding rates were assessed over a short period of time, food levels were still too high to detect significantly different feeding rates between species. Also in both experiments, like those in the late spring and early autumn experiments, unfiltered *in situ* seawater was used thus adding to the potential edible particles for the mysids. Seawater POC levels during these experiments ranged from 0.16-0.37 $\mu gC\ mL^{-1}$, but these values may only reflect potential ingestable food. In mid-winter, for instance the seawater samples were dominated by particulate macroalgae which might not be edible for mysids as suggested by their grazing rates on algal detritus. Starving mysids prior to feeding may also explain these results. It is reasonable to expect that the starved mysids might have rapidly filled up their stomachs with whatever edible food was available. The influence of the inherent variability of mysid feeding rates between chambers could not be ruled out.

Although the three mysid species displayed similar feeding rates on the food types offerred, strong preference for *Artemia* sp. nauplii was clearly demonstrated in both mid-autum and mid-winter experiments. The concentration of nauplii was similar in both experiments, thus the lower rates in winter were probably due to the low water temperature (Table 5.1). Like those in the early spring and early autumn experiments, the three mysid species showed a weak selection for both small (*Isochrysis galbana*) and large (*Scrippsiella trochoidea* Stein) sized phytoplankton, and the algal detritus mixed with these phytoplankton. In contrast, the high feeding rates on algal detritus when paired with the zooplankton food type was unexpected and surprising. This might be due to the fact in these chambers, mysids were feeding heavily upon *Artemia* sp. nauplii. The presence of the preferred food type in the suspension may have heightened the "desire" to feed resulting in the greater capture and ingestion rates of

algal detritus. This aroused state might be brought about by highly sensitized visual and mechanoreceptors in response to the swimming nauplii. Organic and inorganic chemicals which leach from the prey most likely stimulated olfactory receptors of the mysids. Reduced rejection rates of algal detritus may have also occurred in these stimulated mysids.

Using a similar radiolabelling technique, Gottfried and Roman (1983) estimated daily ingestion of ^{14}C-labelled coral-mucus detritus in the reef mysid *Mysidium integrum* to range from 1-70% bodily carbon. Although *M. integrum* showed a reasonable ingestion of both substrate and epiphytic bacteria, they noted that labelling the surface bacteria with ^{3}H-thymidine may not be as sensitive as labelling the mucus substrate. If we convert their data to hourly ingestion rates in *M. integrum*, ingestion rates in the three mysid species fall within a similar range.

The study by Mullin and Roman (1986) showed that the reef species *Anisomysis* sp. preferred animal prey (carnivory), as represented by the nauplii of *Artemia* sp. The same mysid species can ingest 1-6 nauplii (mysid h)$^{-1}$, and the mysid may be satiated after ingesting 4 nauplii which is equivalent to 3.2 μgC (mysid h)$^{-1}$ or 3% of mysid bodily carbon. The fact that the average mature *Paramesopodopsis rufa* is 2-4 mm longer than mature *Anisomysis* sp. (5 mm eye-to-telson length) may explain the almost double percentage bodily carbon intake observed in *P. rufa* ingesting the nauplii of *Artemia* sp. *Anisomysis* sp. also ingested algal particles in relatively high quantities, which indicates that this species is an efficient large particle feeder. Mullin and Roman (1986) categorized *Anisomysis* sp. as a selective carnivore and at the same time a macrophagous detritivore. The evidence provided in the present study suggests that the three mysid species fall within the same feeding category.

Factors that may influence accuracy and effectiveness of the radiotracing technique are many. These limitations, when taken into account, would increase the robustness of information that can be extracted from the study. Differential uptake of the radioactive label within and between food types would probably contribute most of the variability of the amount of label in the food. Although the 20-min incubation time (less than the minimum food gut passage time) has circumvented problems of

underestimation due to egestion of radiolabelled food, the magnitude of respired $^{14}CO_2$ (not measured in the present study) remains a problem. Problems related to loss of incorporated ^{3}H-thymidine through respiration seem remote as the label is incorporated in DNA (Roman and Rublee 1981; Fuhrman and Azam 1982). Another possible source of underestimation may be through loss of incorporated radiolabels in food into the surrounding medium during processing by the mouthparts due to the manner in which mysids macerate and grind food using their mandibles (Lasenby and Langford 1973). However, this might not be an important factor since minimal loss of dissolved organic carbon has been reported as a result of sloppy feeding on large diatoms by *Mysis relicta* (Sierszen and Brooks 1982).

A range of factors may influence grazing rate, which Roman and Rublee (1981) enumerated: chemical composition of particles, particle size distribution, particle size retention and efficiency of the animal feeding. By injecting an appropriate concentration of ^{14}C and ^{3}H labels into Haney chambers containing naturally occurring zooplankton and both autotrophic and heterotrophic potential food particles, Roman and Rublee (1981) have observed higher ingestion rates for ^{14}C-labelled autotrophs than for ^{3}H-labelled particles. The ratio of the grazing rates on ^{3}H-labelled particles to ^{14}C-labelled particles was an average of 0.27. Although there was significant grazing on ^{3}H-labelled particles (range = 1.92-97.68 L [mg zooplankton AFDW]$^{-1}$ d^{-1}), rejection of these particles might have resulted in the great difference between grazing rates of the two food particle types (Roman and Rublee 1981).

Feeding efficiency of *Neomysis mirabilis* on plant and animal detritus, melanin and the peridinean *Gymnodinium kowalevskii* estimated using the radiocarbon method has been examined by Pechen'-Finenko and Pavlovskaya (1975). *N. mirabilis* showed a strong preference for live *Gymnodinium* in all food types offered. Very low ingestion of algal detritus may be explained by its very long aging period (4 months) used in their study. Age of algal detritus has been shown to influence its ingestion rate in the copepod *Acartia tonsa*, in that very old detritus particles became reduced below optimum size due to the action of microbiota (Roman 1977). This is supported by Roman's (1977) finding that *A. tonsa* showed significantly high ingestion on 14-day

old and least on 56-day old *Fucus vesiculosus* detritus. Furthermore, laboratory prepared algal detritus may not actually reflect the detritus encountered by these animals in the field or the animals may have some obligate nutritional requirements for food sources other than algal detritus (Roman 1977).

Alternatively, perhaps an optimal macrophyte detritus (size and quality) is needed to elicit digestive enzymes as shown in *Mysis stenolepis* feeding on unaged seagrass detritus (Foulds and Mann 1978). Very high ingestion rates on unaged *Spartina* detritus have also been reported in *Neomysis americana* (Zagursky and Feller 1985). *M. stenolepis* has been confirmed to depend on gut microflora (Wainright and Mann 1982) to digest and assimilate cellulose, and is also capable of synthesizing endogenous cellulase (Friesen *et al.* 1986).

This study presents mysid consumption of particulate food prepared in the laboratory. The importance of protists and unattached bacteria (Zagursky and Feller 1985), and dissolved organic matter (DOM) from water drinking (Fox 1952), all known to form a significant proportion of ingested food among suspension feeders, are not included in the feeding rates reported here. Feeding rate estimates are average values calculated from the collective feeding performance of all individuals enclosed in the chamber. There will always be individuals not feeding or which did not have the chance to capture food. This applies in particular to the feeding on the animal prey which might have been aggregated. Low feeding rates on randomly distributed phytoplankton cells and algal detritus may be explained by the mysid behavioural response such as rejection and/or poor capture efficiency on smaller particulate food.

Although the manner in which the field experiment were carried out approximated the natural conditions of light, temperature, and water chemistry, enclosing mysids in chambers excludes them from the currents they normally experience (Mullin and Roman 1986). The only source of motion inside the chamber would come from the to and fro wave action. Variability in mysid clearance rates may be attributed to the already present or dominant food particles in the enclosed water. From rough estimates of relative abundance of particles, amorphous detrital materials dominate in freshly collected water samples from experimental sites. Difficulty in

enclosing similar numbers of mysids in each chamber is reflected in the variability in number of mysids in grazing chambers (Table 5.1). Intraspecific competition for food is probably a lot stronger in chambers with higher numbers of individuals, and consequently may reduce per capita feeding performance (Folt 1985).

Although a fairly limited time and space window on the feeding behavioural repertoire of the three co-occurring mysid species has been addressed, the present study demonstrates that they ingest a wide range of food (omnivory) and that they show a strong preference for the animal particulate food, *i.e. Artemia* sp. nauplii. The three mysid species also ingest algal detritus particles. Although they consume essentially similar types of food, some degree of feeding selectivity may be occurring. *Paramesopodopsis rufa* has been shown to display a tendency for carnivory, but this was not explicitly shown in this study. *Tenagomysis tasmaniae*, limited by some behavioural attributes, may rely more on algal detritus and phytoplankton cells and least on live zooplankton. *Anisomysis mixta australis* showed an unrealistic clearance rate on zooplankton, very low values on phytoplankton cells, and moderate rates on algal detritus. *A. mixta australis* may therefore be a microphagous feeder that is efficient at consuming smaller/finer particles, *i.e.* algal particles < 63 μm, as indicated by this study. Very similar food requirements between the three mysid species imply strong competition for similar food resources, and this similarity was pronounced when the three mysids were starved.

CHAPTER 6

ASSESSMENT OF HERBIVOROUSNESS USING THE DIGESTIVE ENZYME LAMINARINASE ASSAY

Introduction

The spectrum of digestive enzymes in zooplanktonic crustaceans has been thought to provide insights into the nutritional history of the organism being studied (*e.g.* Mayzaud and Poulet 1978; Mayzaud and Mayzaud 1981; Mayzaud *et al.* 1985; Mayzaud 1986). Two groups of enzymes are usually analyzed: the group I or central metabolic enzymes which exhibit heterozygosity positively correlated with environmental heterogeneity, and the group II enzymes which metabolize externally derived substances and with heterozygosity positively correlated with the phyletic diversity of trophic resources (Nelson and Hedgecock 1980).

However, there are conflicting issues in zooplankton enzyme studies. Particulate organic matter in seawater as a measure of available food, and field estimates of enzyme activity were either found correlated (Boucher *et al.* 1976; Mayzaud and Conover 1975; Mayzaud and Poulet 1978; Hirche 1981) or not (Head and Conover 1983; Hassett and Landry 1983,1988; Båmstedt 1988). Digestive enzymes are either instantaneously induced by the presence of the complementary substrate (Mayzaud and Poulet 1978; Cox 1981; Cox and Willason 1981; Samain *et al.* 1981; Mayzaud *et al.* 1985; Willason and Cox 1987) or not necessarily substrate specific (Head and Conover 1983; Head *et al.* 1984; Hassett 1994). These conflicts arose because digestive enzyme activity is a complicated matter, and the process is governed by several factors which include the organism's feeding history (acclimation to food abundance and types), life history (developmental stages, sex), feeding periodicity, and food environment periodicity (Head *et al.* 1984; Mayzaud 1986). Superimposed on these factors are short, medium, and long term variations of enzyme production (Head *et al.* 1984; Mayzaud *et al.* 1985). The results obtained depend upon which combinations of factors prevail.

Herbivorous feeding in marine zooplankton may be best examined using the activity of the enzyme laminarinase as an index because the purely carnivorous species do not display any significant level of activity (Mayzaud 1986). Analysis of the level of protease activity is an ideal complement but its utility is hampered by its low specificity (Mayzaud 1986). Laminarinase belongs to a class of extra-cellular digestive enzymes capable of hydrolyzing high molecular weight substrates, and is more positively linked with the concentration of potential food in the environment than enzymes for low molecular weight substances such as maltase and cellobiase (Roche-Mayzaud *et al.* 1991). It is ubiquitous, and is very common among bacteria, actinomycetes, and microbial fungi (Bull and Chesters 1966), but may also occur in various soil and litter invertebrates (Nielsen 1963). It comprises a multienzyme system which includes exo- and endo-hydrolytic β-1-3 glucanases and β-glucosidases (Bull and Chesters 1966; McConville *et al.* 1986). Fifty six percent of the enzyme complex is of the endohydrolytic type yielding laminadextrins as initial products, 25% of the exohydrolytic type which yields glucose as the sole initial product, and 19% intermediary products (Nielsen 1963). The enzyme is membrane bound so there is little if any appreciable enzyme activity loss from fluid loss in net damaged material, and it is stable to repeated thawing and freezing (Cox 1981). The enzyme can be induced and the mechanism of induction is by *de novo* synthesis occurring in response to carbohydrate dietary levels (Machis-Mouren *et al.* 1963 cited in Cox and Willason 1981).

Laminarin has been reported to be rather abundant in brown seaweeds and euglenids (Bull and Chesters 1966; Handa and Tominaga 1969). Contained in storage vacuoles in marine macroalgae and phytoplanktonic Chrysophyceae, laminarin is a storage form of carbohydrate which is composed of soluble and insoluble β-1-3 linked D-glucans (Cox 1981; Bull and Chesters 1966). Diatoms (Bacillarophyceae) store laminarin as leucosin or chrysolaminarin which is mainly water soluble and easily degraded in the water column (Handa and Tominaga 1969; Cox 1981). Chrysolaminarin has a degree of polymerization (DP) of 21 which falls within the 20 to 28 DP range of the brown seaweed laminarin (Handa and Tominaga 1969).

Taxonomic differences within the zooplankton have prevented the use of enzyme activity measurements as a direct quantitative estimate of field ingestion rates (Mayzaud 1979.1986; Båmstedt 1988). This is simply because to take one value for the whole assemblage ignores the fact that each component species shows different enzyme activity levels which also vary in different ecological circumstances. The differences in feeding adaptation and ethology of these organisms need to be recognized (Mayzaud *et al.* 1984).

Studies on the digestive enzyme activity of co-occurring zooplanktonic crustaceans with similar potential feeding habits are quite rare. For example, laminarinase activity in two western Pacific Ocean euphausiids indicated higher herbivorous feeding on phytoplankton in *Euphausia pacifica* than in *Nematoscelis difficilis* (Willason and Cox 1987). Although known to be omnivorous, the Antarctic krill *Euphausia superba* has shown higher affinity for phytoplankton than another southern ocean euphausiid *Thysanoessa macrura* from assays involving the enzymes amylase, cellulase, galactosidase and laminarinase (Mayzaud *et al.* 1985). In contrast, Head *et al.* (1984) did not find significantly different laminarinase, amylase and protease activity levels between two neritic calanoid copepod species indicating very similar omnivorous feeding habits.

Digestive enzyme studies in peracarids have been devoted to single species. For example, amylase and laminarinase activity assays have shown that, in the mudflat amphipod *Corophium volutator*, switching from feeding on benthic diatoms to less nutritious macrophyte detritus occurs during winter when diatoms become scarce (Stuart *et al.* 1985). Mayzaud (1986, Table 4.12) categorized the mysid, *Siriella armata* as one of the purely carnivorous zooplankton species which showed no detectable laminarinase activity. Båmstedt (1988) observed high trypsin/amylase ratio in the deep sea mysid *Boreomysis arctica* despite being categorized as an omnivore. Very recently, Kerambrun and Guérin (1993) examined temporal variation of amylase activity as a consequence of starvation and feeding on three artificial food types in the nearshore mysid *Leptomysis lingvura.*

The present study aims to assess herbivorousness in three co-existing mysid

species by measuring laminarinase activity levels both *in situ* and in laboratory feeding experiments.

Materials and Methods

Measurements of Laminarinase Activity in Freshly Collected Mysids

Collection of Animals

Mysids were collected from off Taroona Beach (the same study site described in chapters 2 and 5) on 22 October 1993, and on six occasions in 1994 (10 February, 10 May, 8 July, 11 August, and 6 November). Other details of the collection are given in chapter 2. Captured mysids were immediately sorted to species by careful scooping using a 250 μm mesh nylon sieve. Thirty to thirty five mysids were carefully hand-picked using forceps, and transferred to a sheet of parafilm which in turn was placed in dry ice for snap freezing (-40°C). Mysid collection and sorting were done from 1030 to 1145 H, with the actual capture duration of the animals lasting 20 min. Samples were transported to the Zoology Department of the University of Tasmania and stored at -20°C until the enzyme assay, which was performed 2-3 days after mysid collection.

Laboratory Methods

The laboratory methods used in the present study are similar to those outlined by Willason and Cox (1987). Mysid samples were thawed, and after blotting lightly onto tissue paper, a group of 10 adult mysids was weighed to the nearest 0.1 mg. Individuals of both sexes were mixed because most often females dominated the samples, but whenever possible all three species were sorted according to sex. Since this study examines laminarinase activity of mysids in groups not on a per animal basis, 10 individuals serve as a replicate.

Soon after weighing, mysids were placed into a 25 mL glass hand tissue grinder for homogenizing in 0.25M succinic acid buffer (isotonic with seawater at pH

5) at 4°C. Preliminary analysis showed that this buffer is equally useful as the commonly used Tris-HCl buffer (two-factor ANOVA, F (between buffers) = 1.28, df = 1, $p > 0.05$, F (interaction between species) = 0.204, df = 2, $p > 0.05$). Volume of succinic acid buffer was 1 mL per animal. Homogenization was standardized at 12 strokes for 1 min. In the present study, homogenates were immediately assayed, however, Willason and Cox (1987) noted that they can be stored for 3 weeks at -20°C. In contrast, Mayzaud (1986) noted a significant reduction of activity in 4-day old samples in succinic acid buffer stored at -20°C. Three replicate aliquots were added to pure (95%), soluble laminarin extracted from the brown alga *Laminaria digitata* (Sigma Chemical Company, U.K.) at a concentration of 2.5 mg mL^{-1}. This laminarin concentration has been reported to saturate enzymes in other crustaceans (Cox 1981; Willason and Cox 1987). A preliminary analysis showed that a weight of pure laminarin ranging from 0.5 to 1.0 mg saturated the enzyme laminarinase in a 200 µL homogenate from each of the three species (Fig. 6.1). In the present study 200 µL of the mysid homogenate was mixed with 0.6 mg laminarin. A fourth aliquot was without the substrate to serve as the mysid tissue blank. To account for glucose impurities in the substrate, and to test whether the test kit enzyme reacted with the pure laminarin, 0.5 mg laminarin was dissolved in 200 mL of the buffer. This was assigned as the laminarin blank. All mysid homogenate aliquots and the laminarin blank were agitated for 10 s and quickly transferred to an oven set at 37°C (±1) for 60 min.

The reaction was stopped by immersing the samples in an ice bath and adding 100 µL of 2°C distilled water. Samples were immediately centrifuged for 5 min at 13000 rpm. 140 µL of supernatant was withdrawn and transferred to 10 mL polyethylene tubes and assayed using the Boehringer-Mannheim Glucose Test Kit®: *i.e.* the GOD-Perid® method. The glucose concentration of supernatants was calculated from a glucose calibration curve obtained by using the same glucose test kit. The resulting calibration curve is expressed by the following equation ($r^2 = 0.999$, $p < 0.0001$):

$$\text{glucose concentration (mg/100ml)} = \frac{\text{(blanks corrected absorbance - 0.018)}}{0.02},$$

where blanks include absorbance from the distilled water, mysid tissue, and undigested laminarin.

The activity of the enzyme laminarinase (ELA) was expressed as μg glucose min^{-1} g mysid wet $weight^{-1}$.

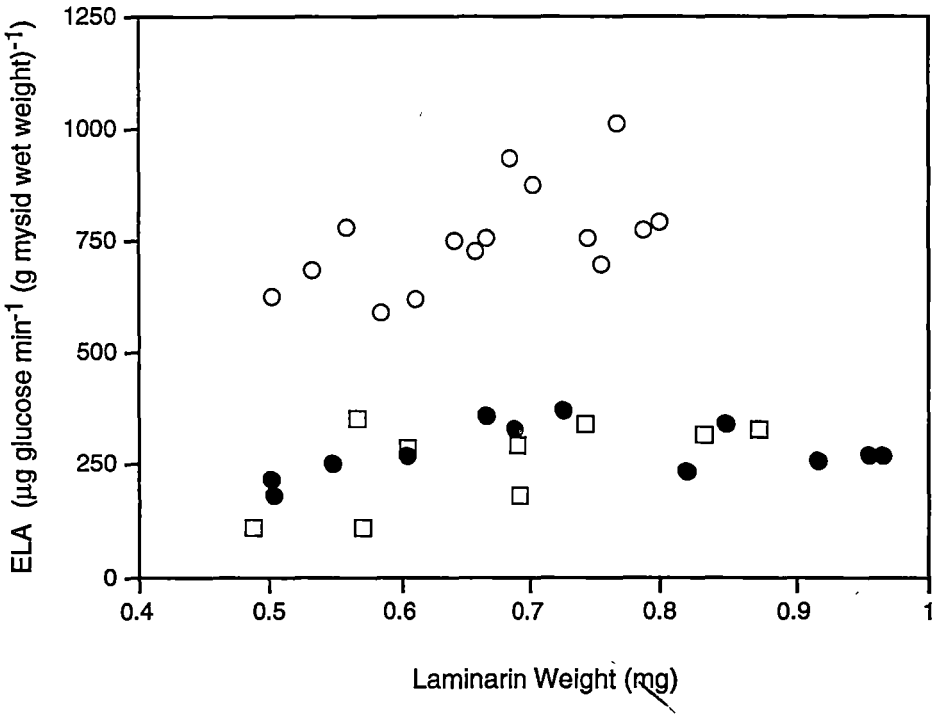


Figure 6.1 Saturation of enzyme laminarinase activity (ELA) over the range of laminarin substrate used in the assay. Squares - *Anisomysis mixta australis*, closed circles - *Paramesopodopsis rufa*, open circles - *Tenagomysis tasmaniae*.

Laboratory Experiments

The Effect of Starvation and Feeding on *Scrippsiella trochoidea* Stein

On August 1994 (late winter), I examined the ELA levels of the three mysid species in response to short term (24 hours) starvation, and medium term (10 days) feeding with the dinoflagellate *Scrippsiella trochoidea* Stein which synthesizes and

stores amylose. This experiment addresses the question of whether a non-laminarin storing microalga would decrease laminarinase activity levels in the three mysid species over time.

A randomized block design was employed for this experiment. A cell comprised a container with one of the three mysid species. Ten adult individuals from one of the three mysid species were pipetted into a 2-litre green plastic container which contains 5 µm Millipore-filtered seawater with 31.6 ‰ salinity. For the entire 10-day experiment, 5 containers for each mysid species were set-up. Three replicate blocks were set-up for *Paramesopodopsis rufa* and *Tenagomysis tasmaniae*, and only two for *Anisomysis mixta australis* because few individuals of this species were caught during field sampling. Laminarinase activity was measured every two days on all animals remaining in the container assigned to a particular day.

The experiment was performed at a water temperature of 12 ± 2°C and a 12-h light and 12-h dark photoperiod. All animals were initially starved for 24 h. The day 1 data for each mysid species were ELAs from starved individuals. The remaining animals were then fed daily with 1.6-2.1 x 10^4 cells ml^{-1} of *Scrippsiella trochoidea* Stein in its logarithmic growth phase. Before adding the fresh food, dead mysids from each container were removed and the stale seawater was replaced by carefully decanting leaving enough for the remaining mysids to swim. The container was covered with a 300 µm nylon mesh which prevented mysids from escaping during decanting.

The Effect of Feeding on *Artemia* sp. Nauplii

ELA of immature individuals of the three species, which had grown from the juvenile stage using *Artemia* sp. nauplii (see chapter 7 on growth studies), was analyzed. This was carried out to determine the effect of zooplankton diet on the laminarinase activity in the three mysid species.

The analysis of laminarinase activity in these experiments followed the same procedure as in the determinations on freshly collected mysids.

Statistical Treatment

ELA variation over time and between the three species was analyzed using a two-factor ANOVA with time (sampling date for the field determinations and day for the medium term feeding experiment) and mysid species as the two independent variables. The means model ANOVA was used for the results from the starvation and phytoplankton feeding experiment because of missing cells in the data due to the mortalities of mysids. Significant variations of these factors were followed by a simultaneous multiple comparison of means using Tukey's Honestly Significant Difference test. All statistical analyses were done using SYSTAT vers. 5.2 program for Macintosh computers (Wilkinson 1992).

Results

Figure 6.2. shows the distinct sizes of the three species (two-factor ANOVA, $F = 281.67$, df = 2, $p < 0.001$) with *P. rufa* being the largest, *T. tasmaniae* intermediate, and *A. mixta australis*, the smallest. Much of the size variability between sampling dates ($F = 39.57$, df = 5, $p < 0.001$) was attributed to the significantly smaller *P. rufa* individuals in July (mid-winter) compared to the other months ($p <$ 0.05 for all). *T. tasmaniae* was also smaller in July ($p < 0.05$). Size within each mysid species at all sampling dates showed very low variability (CV < 9.4 %). The difference of laminarinase activity within mysid species due to sex was only tested in *T. tasmaniae*. In three months' data (October 1993, and August and November 1994), a highly significant variation of ELA between sexes was mainly due to sampling date (two-factor ANOVA, $F = 25.157$, df = 3, $p < 0.001$), but not between sexes (Tukey's HSD test, $p > 0.05$ for all). From all six sampling dates, undigested laminarin did not react with the test kit as shown by very low laminarin blank values which are comparable to the distilled water blank values ($p > 0.05$, Scheffé's F-test). This means that the test kit used here is equally as effective as the Sigma Glucose Assay Kit commonly used in other studies in the glucose concentration assay (Cox 1981; Head *et al.* 1984; Willason and Cox 1987). Mysid tissue blanks differed

significantly ($p < 0.01$, Scheffé's F-test) from the distilled water blanks suggesting the indispensability of this blank as a correction factor in the final laminarinase activity calculation. Since aliquot readings from replicate mysid homogenates were fairly similar, these values were averaged to represent the ELA of one replicate mysid sample.

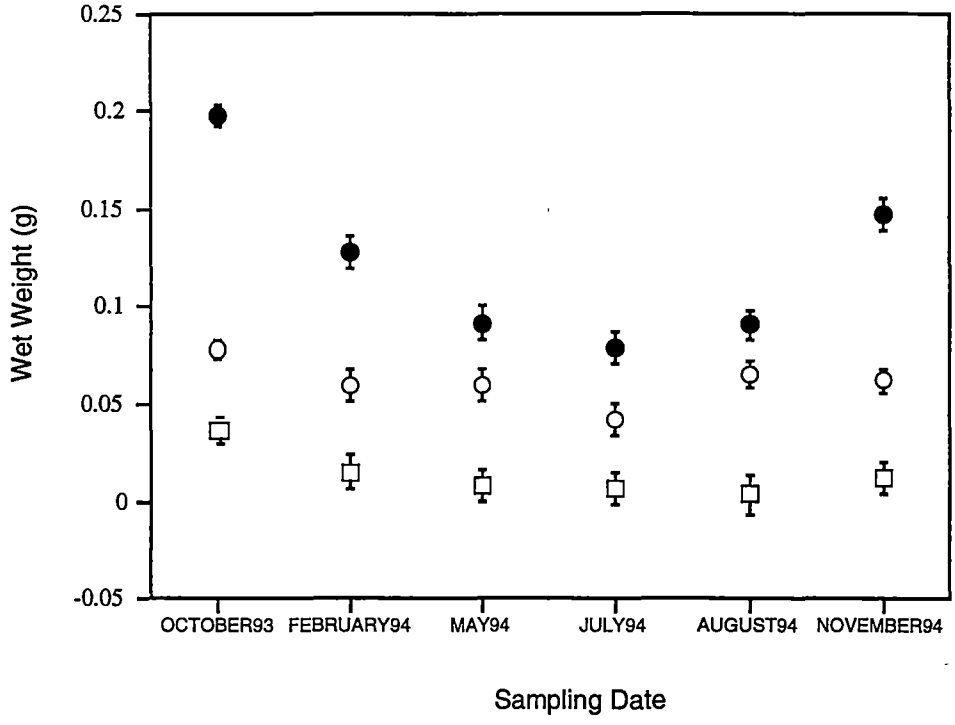


Figure 6.2 Temporal variation in average wet weight in the three mysid species over six sampling dates. Error bars: standard error. Squares - *Anisomysis mixta australis*, closed circles - *Paramesopodopsis rufa*, open circles - *Tenagomysis tasmaniae*.

Temporal Variation of ELA

Figure 6.3 shows the laminarinase activity in the three species over six sampling dates. ELA varied significantly between sampling dates ($F = 19.43$, df = 5, $p < 0.001$) and between species ($F = 125.35$, df = 2, $p < 0.001$). A highly significant interaction of these factors was also shown ($F = 5.29$, df = 10, $p < 0.001$). Between species variations are due to the 1.8 to 4.7 times higher average ELA in *T. tasmaniae* than in *P. rufa*. In addition, ELA in *A. mixta australis* varied widely with its lowest average of 261.1 ± 103.9 SD comparable to some values recorded in *P. rufa*, and the

highest average of 592.2 ± 95.44 SD which is comparable to those in *T. tasmaniae*. The average ELA in *T. tasmaniae* ranged from 423.6 ± 192.7 SD to 777.533 ± 52.89 SD, while those in *P. rufa* ranged from 118.3 ± 6.7 SD to 301.4 ± 50.98 SD.

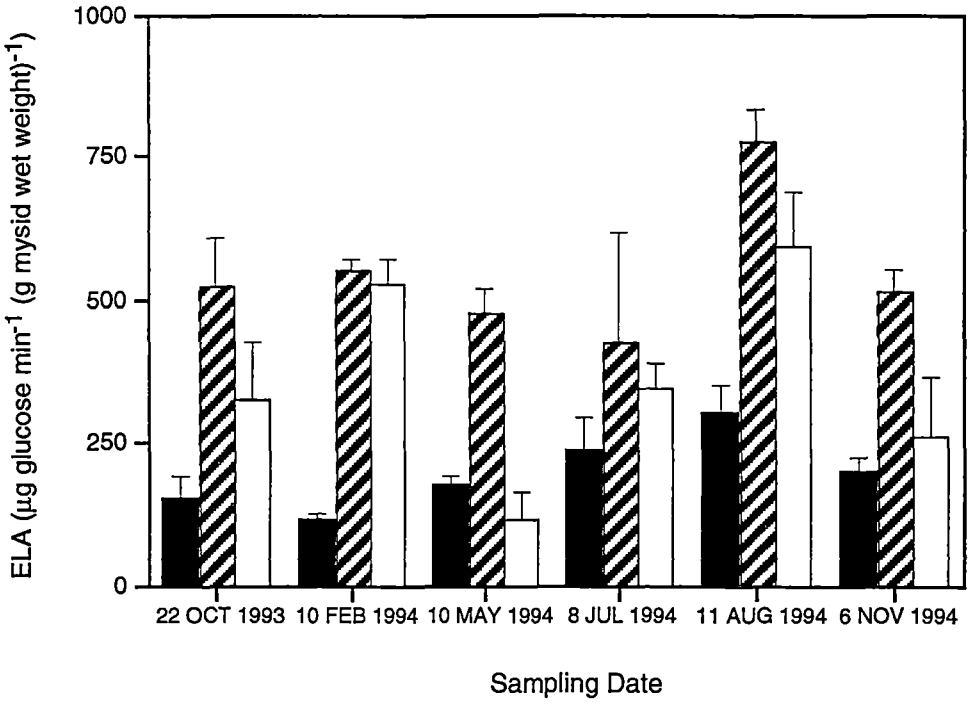


Figure 6.3 Temporal variation of average laminarinase activity (ELA) in three co-occurring mysid species. Error bars: standard deviation. Open bar - *Anisomysis mixta australis*, solid bar - *Paramesopodopsis rufa*, hatched bar - *Tenagomysis tasmaniae*.

The similar high ELA levels in *T. tasmaniae* were sustained at all sampling dates, but peaked in August ($p < 0.05$ when compared with values from other months). High ELA activities in this species were similar to those in *A. mixta australis* in February, July and August ($p > 0.05$). The ELA in the two species differed significantly in October, May, and November ($p < 0.01$). Except in the July ELA, values for *T. tasmaniae* and *P. rufa* differed significantly ($p < 0.01$).

Although ELAs in *P. rufa* at all sampling dates were similar ($p > 0.08$), the highest ELA in August might represent a peak as it gave the lowest p value (= 0.08) when compared with the ELA in other months. Similar ELAs in both *P. rufa* and *A.*

mixta australis occurred in May, July, and November ($p > 0.05$), but the ELA of the two species differed significantly in October, February, and August ($p < 0.01$).

ELAs in *A. mixta australis* peaked twice (February and August) and these are not significantly different ($p > 0.05$). Except for February, the ELA of this species in August differed significantly from the rest of the sampling dates ($p < 0.05$). In this species, the sampling dates with significantly different ELA were between October and February, October and May, February and May, February and November, and May and July.

Laboratory Experiments

The Effect of Starvation and Feeding on *Scrippsiella trochoidea* Stein

The day 0 data of this experiment (Fig. 6.4) are identical to those on 11 August 1994 (data from Fig. 6.3), because this was the date of collection of the mysids used in this experiment. Day 0 ELA served as the *in situ* levels and at the same time the reference point for the activities of both starved and fed animals. Highly significant variation of ELA from this study ($F = 27.49$, df = 13, $p < 0.001$) was explained by the highest activity in *T. tasmaniae* ($p < 0.01$ for all) compared to the other two species. Although starved *T. tasmaniae* and *A. mixta australis* did not show a significant decrease ($p > 0.05$ for both) after 24 h compared to the *in situ* levels, the former species showed increased variance which was not observed in *A. mixta australis*. The ELA of 24 h-starved *P. rufa* sharply declined ($p < 0.05$) compared to the day 0 values. No mortalities were observed after 24-h deprivation of food in the three mysid species.

After two days of feeding, only the variance of the ELA in *P. rufa* decreased but the average value remained the same as those in starved animals (day 1). Data for this species were collected only up to day 3 because mortality was greater than 50%, and five individuals was considered a minimum for the enzyme assay . On day 3, ELA in *P. rufa* was lowest compared to the other two species, followed by *A. mixta australis* whose ELA remained similar to those measured in starved animals. *T.*

tasmaniae showed the highest ELA, but these values were not significantly different from those on days 0 to 1. On day 5, the average and variance of the ELA in *A. mixta australis* decreased significantly compared to earlier levels ($p < 0.05$). These values were still much lower compared to those in *T. tasmaniae* which showed only a decrease in variance in their ELA. On day 7, the average ELA in *A. mixta australis* showed a dramatic increase in variance which made these values not significantly different from the previous ones. Again, these values are still significantly lower than those in *T. tasmaniae*. The average ELA in *T. tasmaniae* on day 7 remained the same, but its variance was lowest. A significant decrease of ELA in this species was only observed on day 9, at which time measurements for this species ended.

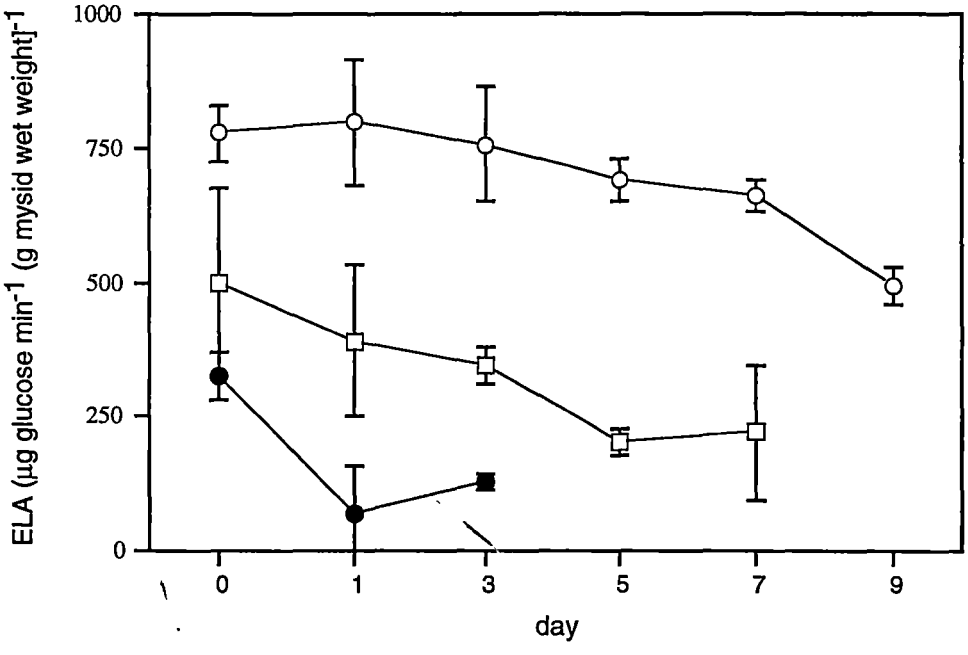


Figure 6.4 Medium term change of enzyme laminarinase activity (ELA) in the three co-occurring mysid species. Day 0 represents *in situ* levels, day 1 after 24 h starvation, and for the rest of the experiment animals were fed with *Scrippsiella trochoidea*. Error bars: standard deviation. Squares - *Anisomysis mixta australis*, closed circles - *Paramesopodopsis rufa*, open circles - *Tenagomysis tasmaniae*.

The Effect of Feeding *Artemia* sp. Nauplii

ELA in immature individuals of the three species from the growth study is shown in Table 6.1. All three species showed comparable ELA (Kruskal-Wallis test,

$H = 3.6$, df = 2, $p > 0.05$). The reduced activity in *A. mixta australis* was lower than in the *in situ* measurements using immature individuals of this species and in *P. rufa*. Likewise, those in *T. tasmaniae* are significantly lower than their *in situ* values, but were comparable to those *in situ* values in *P. rufa*.

Table 6.1 Enzyme Laminarinase activity (ELA) (μg glucose min^{-1} [g mysid wet $weight]^{-1}$) of immature individuals fed with *Artemia* sp. nauplii in a laboratory growth study (Chapter 7). Values in parenthesis are *in situ* ELA. A replicate (n) represents 10 individuals.

Mysid Species	mean ± SD	n
Anisomysis mixta australis	64.00 ± 7.69	2
	(313.87 ± 20.40)	3
Paramesopodopsis rufa	76.92	1
	(146.13 ± 100.79)	3
Tenagomysis tasmaniae	105.72 ± 14.36	2
	(547.83 ± 19.91)	3

Discussion

The laminarinase activity levels of the three mysid species are similar to those reported by Willason and Cox (1987). The values obtained for *Paramesopodopsis rufa* and for *Anisomysis mixta australis* are of similar magnitude to those obtained in *Nematoscelis difficilis* females which consumed smaller amounts of phytoplankton (less herbivorous feeding) compared to the females of *Euphausia pacifica*. Values recorded in *E. pacifica* at their nocturnal feeding peak are comparable to those in *Tenagomysis tasmaniae* and the high levels in *A. mixta australis*.

Seasonal and 24 h dietary data for *P. rufa* showed a lower proportion of plant (macroalgal and phytoplankton) material than animal material (crustacean remains) in their stomachs (Fenton 1986). This may account for the weaker ELA levels in this species as shown in the present study which suggests a low reliance on herbivory.

Detectable ELA levels in this species may be interpreted as an adaptation to the gut contents of herbivorous prey (Mayzaud 1986; Båmstedt 1988). Fenton's (1986) study also revealed a very high proportion of macroalgal particles in the gut contents of *T. tasmaniae*. This information agrees with the very strong laminarinase activity obtained from present enzyme assay suggesting the greater importance of herbivory in this species. Whether they mainly feed on macroalgal tissue or on phytoplankton which stores a similar form of laminarin substrate is a very interesting aspect to examine in further studies. The gut contents of *A. mixta australis* was dominated by fine particulate organic matter and a small proportion of crustacean remains (Fenton 1986). This species may be regarded at times either as a phytoplankton-feeder being a non-substrate specialist, or a macroalgal-feeder as in *T. tasmaniae* but which specializes on finer or smaller particles. The latter is more likely as indicated by very similar carbon and hydrogen stable isotope values compared with those of *T. tasmaniae* (Fenton 1986).

The peak in February (late summer) shown by *A. mixta australis* reflects similar high levels of consumption of both macroalgal and laminarin producing phytoplanktonic particles. The reduced level in May in this species may be related to its overwintering habit (Fenton 1992). Head and Conover (1983) observed a similar result with the overwintering calanoid copepod, *Calanus hyperboreus.* In this copepod, the decline in enzyme activity was explained by the degeneration of enzyme secreting cells. This is very unlikely in *A. mixta australis* as their reduced ELA levels are comparable to those in *P. rufa*, indicating that they still possess functional but depressed enzyme secreting cells.

Significant interaction between species and sampling date suggests that the peak of activity in August (late winter) may be associated with all three species ingesting relatively high levels of laminarin based particles. These particles may include both macroalgal detritus, suspended through winter, and phytoplankton as diatoms near the site where mysids were collected usually have already bloomed in this month (Hallegraeff 1994, pers. comm.).

The decrease in ELA in both *P. rufa* and *A. mixta australis* after 24 h starvation

was similar to those observed in copepods and euphausiids (Cox 1981; Cox and Willason 1981; Roche-Mayzaud *et al.* 1991). In contrast, Kerambrun and Guérin (1993) observed a decline in amylase activity after one day starvation in *Leptomysis lingvura* . Differences in the species and enzymes being studied may explain these dissimilar results. Furthermore, McConville *et al.* (1986) observed elevated laminarinase activity in starved *Euphausia superba* after 12 h. This might have been detected if ELA was examined in the two mysid species after 12 h. McConville *et al.* (1986) also noted that the exo-acting glucanase component was responsible for the increased activity. It is likely then that the two mysid species synthesize smaller proportions of this component enzyme than *E. superba*, and that during starvation the response of this enzyme was not manifested.

The decrease in ELA on day 9 in *T. tasmaniae* should not be interpreted as a response to a non-laminarin storing phytoplankter because it is quite possible that *T. tasmaniae* can sustain high levels of activity for prolonged periods as suggested in the *in situ* results. Thus the decrease might just be a response shown much earlier in *A. mixta australis* (after 5 d). Had the experiment continued much longer, a recovery of ELA in *T. tasmaniae* similar to that displayed by *A. mixta australis* on day 7 might have occurred. Although *P. rufa* maintained a reduced level up to day 3, suggesting a rapid response to the absence of the laminarin substrate, no definite conclusion can be drawn because of high mortality. It is likely though that because it is highly dependent on animal food (Fenton 1986, see chapters 4, 5 and 7), feeding on plant material is not the right experimental approach in studying this animal's digestive enzyme dynamics.

Most interestingly, *T. tasmaniae* showed a much reduced level of ELA when juveniles were grown for 15 days to immature stages on an *Artemia* sp. nauplii diet. This suggests compensatory response to the quality of available food, *i.e.* mainly protein. The reduced level of ELA in the three species suggests that there exists a background or maintenance level at different developmental stages that are independent of any food cue. Digestive enzyme secretion in various developmental stages of *Penaeus* is food independent, and depends on nutritional needs at a particular stage superimposed on the modification of the gut (Lovett and Felder 1991; Rodriguez

1994). In addition, observations on the three mysid species and in *Penaeus* do not exclude the possibility that enzyme activities may be expressions of vestigial and non-functional characters (Dall and Moriarty 1983).

The patterns of temporal variation of the laminarinase activity in the three species should be perceived as a synthesis of various interdependent factors (Head *et al.* 1984; Mayzaud 1986). At the level of cells and organs, digestion and assimilation depend upon the dynamics of the digestive cells of the hepatopancreas which are classified into R-cells (cells for absorption), B -cells (cells that synthesize enzymes for intra-cellular digestion), F-cells (cells that synthesize enzymes for extracellular digestion), and E-cells (cells giving rise to F and R cells). Cell structure, types, and function appear to be similar in both mysids and most decapods (Friesen *et al.* 1986; Brunet *et al.* 1994). The processes by which these cells are mobilized are highly complex and independent of other phases of digestion (Roche-Mayzaud *et al.* 1991; Johnston *et al.* 1993). The dynamics of these cells in relation to the digestion process remain unknown (Brunet *et al.* 1994).

Studies have revealed that production of enzymes could be induced suggesting an active response, although after a certain set time lag relative to the abundant and prevalent constituent of food in the environment (Cox 1981; Cox and Willason 1981). Temporal analysis of digestive enzyme activity has indicated that in relation to increasing amounts of food, a time lag of 1-6 days (Willason and Cox 1987), 1/2 day to < 1 week (Hassett and Landry 1983), 1 day (Kerambrun and Guérin 1993), and at least 2 days (Roche-Mayzaud *et al.* 1991) is necessary before an increase of the enzyme becomes apparent. Time lags are not unexpected because suspension feeding animals adjust to medium term- (and perhaps long term-) time averaged food concentration and medium term-time averaged ingestion (Roche-Mayzaud *et al.* 1991).

Time of exposure which is very critical to enzyme response is longer than digestive processes such as food transit, which implies that short term changes in food or substrate level would have little chance of inducing a response. Rates of replenishment of *de novo* synthesized laminarinase may be fast enough (Head *et al.* 1984). Ingestion, digestion, and assimilation are key processes of zooplankton

nutrition governed by feedback mechanisms of the animal's nutritional needs, which are tightly associated with the real control of nutritional acclimation, *i.e.* not food supply but the organism's energy requirement (Roche-Mayzaud *et al.* 1991). Synthesis of enzymes is in part controlled by the action of two antagonistic hormones, or possibly by the neuro-endocrine system which regulates the physiology of ingestion and digestion (Mayzaud *et al.* 1984). Here the influence of environmental cues on various sensory modalities in the organism operates.

High values may either be a reflection of a much higher feeding activity for a particular food item in the most recent past (Cox and Willason 1987) or the quality of food ingested (Mayzaud and Poulet 1978; Boucher *et al.* 1975; Mayzaud and Conover 1975), or by some internal biological clock (Mayzaud *et al.* 1984). On the contrary, the food acclimation hypothesis, which states that with abundant available food, the activity of digestive enzymes increases accordingly, has been questioned (*e.g.* Hasset and Landry 1983; Head *et al.* 1984). These authors argued that the animals being studied maintain a certain level of activity as an anticipatory adaptive strategy for future higher concentration of food brought about by a very patchy food environment (Hasset and Landry 1983). Recently, however, Roche-Mayzaud *et al.* (1991) reported that the acclimation time hypothesis still holds but only in food limiting cases, *i.e.* below food saturation or critical concentration point.

Interpretation of these results should be taken with extra caution because studies have noted that activity of laminarinase co-varies with other carbohydrases, *e.g.* amylase (Harris *et al.* 1986). Assays of groups of whole animals as in the present study do not distinguish which laminarinase (synthesized, stored, or secreted) actually reacts with the substrate (Cox and Willason 1987). Nor do they separate the contribution of individual variation within a population (Mayzaud 1986; Head *et al.* 1984).

The major role of microbial flora and fauna which might reside (facultative and obligate) in the guts of *T. tasmaniae*, and aid in the conversion of ingested macroalgal food could not be ruled out. Evidence in mysids supports the idea that *Mysis stenolepis* is capable of digesting cellulose-based detritus solely by endogenous

cellulases (Friesen *et al.* 1985) or with the aid of resident gut microflora (Foulds and Mann 1978; Wainwright and Mann 1982). The role of endogenous laminarinase versus laminarinase from microbes in mysid feeding needs to be examined.

The present study demonstrates an aspect of the feeding ecology of these three co-occurring species, *i.e.* the partitioning of their food resource by differences in the level of herbivorousness. Laminarinase activity measurements have shown overlap in herbivorous feeding in the three coexisting species, however they differ in terms of the intensity of herbivory, and response to the food environment over medium and long temporal scales. The study also demonstrated the possibility that the three species share a baseline level of laminarinase activity which reflects a shared character associated with species belonging to a common phylogenetic ancestor. This baseline level, however, is then modulated by the different feeding adaptations of the three species. This study confirms the findings, and extends Fenton's (1986) conclusions, which were based on stomach contents.

CHAPTER 7

SURVIVORSHIP AND GROWTH STUDIES

Introduction

Somatic growth of an organism is manifested by both increase in size (body length growth) and biomass (specific growth). In mysids, wide ranging factors which drive rates of incremental growth include life history stage, environmental temperature, food availability, salinity, hydrostatic pressure and probably even intra- and inter-specific interactions (*e.g.* Mauchline 1980, 1985; Toda *et al.* 1984, 1987).

Fertilized eggs of mysids develop into larvae within the female's brood pouch (Mauchline 1980,1985; Wittmann 1984). The post-marsupial stage commences when larvae moult into juveniles. Once expelled by their mothers, these juveniles or miniature adults adopt almost immediately an adult life style (Mauchline 1985). Temperature seems to be the most dominant environmental factor controlling further growth and development of post-marsupial stages (Mauchline 1985; Morgan 1985). In contrast, food availability and quality rather than temperature have also been argued to primarily limit mysid growth (Hansson *et al.* 1990). This may be the case as ingestion of the optimal food by feeding stages ultimately results in an optimal growth (Hughes 1980). However, food-limited growth might only be true in predatory zooplankton, but less likely in herbivorous coastal species (Huntley and Boyd 1984). It is also possible that growth rate is dependent on temperature with an interaction superimposed by the different allocation of assimilated food (Toda *et al.* 1987). Morgan (1985) noted that the growth rate of *Mysis relicta* is controlled by a combination of lake productivity and temperature, but since the temperature regimes experienced by most allopatric *M. relicta* populations vary only slightly, the great differences in growth and life history among populations could be food related.

Studies on the growth and development have been done on a few mysid species (Mauchline 1980, 1985). Many of these studies have been undertaken mainly

for toxicity testing (*e.g.* Nipper *et al.* 1993), aquaculture purposes (*e.g.* Léger *et al.* 1986; Reitsema and Neff 1983), and understanding the biology of mysid growth and life history (*e.g.* Clutter and Theilacker 1971; Amaratunga and Corey 1975; Gaudy and Guérin 1979; Asthorsson and Ralph 1984). Optimal utilization of different diets by mysids has been assessed at either the ingestion or assimilation phases of feeding, and again on single species of mysids (*e.g.* Pechén-Fineko and Pavlovskaya 1975; Mullin and Roman 1986). Very recently, Kreeger *et al.* (1991) fed two mysid species from Californian waters four types of diet to compare somatic growth and reproductive output. They found no significant difference in growth between species on the four diets, but greater reproductive output and survival of young in both species was observed with a mixed diet of lipid enriched *Artemia* sp. nauplii, lipid microspheres, and the harpacticoid copepod, *Tigriopus californicus.*

Clutter (1967) noted that if co-existing mysid species which experience similar temperature and other physico-chemical characteristics of their habitat, show similar growth on similar diets and in similar laboratory conditions, it is highly probable that these species may compete strongly for the same limiting food resource unless that resource is partitioned. None of the previous mysid growth studies has addressed the question whether coexisting mysid species exhibit differences in survival and growth when offered different diets. Neither have they investigated the somatic growth response of co-occurring mysid species held together and fed with reduced levels of food which best supports growth. The present study was aimed at answering these questions using three sympatric Tasmanian mysid species.

Materials and Methods

Location of the Study and Mysid Collection

The experiments were conducted on March-April 1994 (early- to mid-autumn) and on September to October (spring) at the Marine Laboratories of the Division of Sea Fisheries, Department of Primary Industries and Fisheries at Taroona, southeast

Tasmania. Situated on the coast, the laboratory is equipped with a flow through system which receives seawater pumped directly from offshore. The culture room where the growth tanks were set-up is supplied with 20 μm rapid sand- and 5 μm Omni-Basic®- filtered and UV-treated seawater. Located just at the back of the Marine Laboratories is a rocky subtidal area where mysids used in my other studies were collected (see Fig. 5.1). Mysids used in the present study were also collected from the same habitat. Aggregations of younger instars (juvenile and immature stages) were located by skin diving, and collected using a 200 μm mesh hand-held scoop net with a rectangular mouth dimension of 25 cm x 17 cm. Captured mysids remained underwater until their quick transfer to 20-L buckets which were then transported to the laboratory. In order to obtain initial sizes of the animals, mysids were anaesthetized using 1 drop of 2% m-amino benzoic acid ethyl ester methanesulfonate (MS222) (Landry 1978; Yen 1982) per mL filtered seawater. Mysids became immobile 2-3 min after contact with the anaesthetic. Anaesthetized mysids were transferred to a plastic Petri dish using a wide bore Pasteur pipette, and their "standard" lengths (tip of carapace rostrum to dorsal tip of the last abdominal segment) measured using a video-microscopy system attached to a Macintosh computer with the image processing program *Image* v1.53b23 (National Institute of Health, USA, 1993). Mysids started to show signs of recovery after 10-15 min, and full recovery was observed after 30-45 min. Fully recovered mysids were starved for 20 h in 1-L plastic containers containing filtered seawater.

Growth Chambers

The growth apparatus was designed as a flow through seawater system. It consisted of nine 4-L black plastic chambers (18.5 cm x 13 cm x 26.7 cm) arranged 3 in a row and 3 in a column inside a 120-L (97 cm x 48 cm x 26 cm) plastic tank (Fig. 7.1A). Seawater delivered to the large tank entered each of the small chambers through 300 μm rectangular mesh windows (30 mm x 20 mm), one on the side facing the incurrent flow (inlet) and one directly opposite to this side (outlet) (Fig. 7.1A,B).

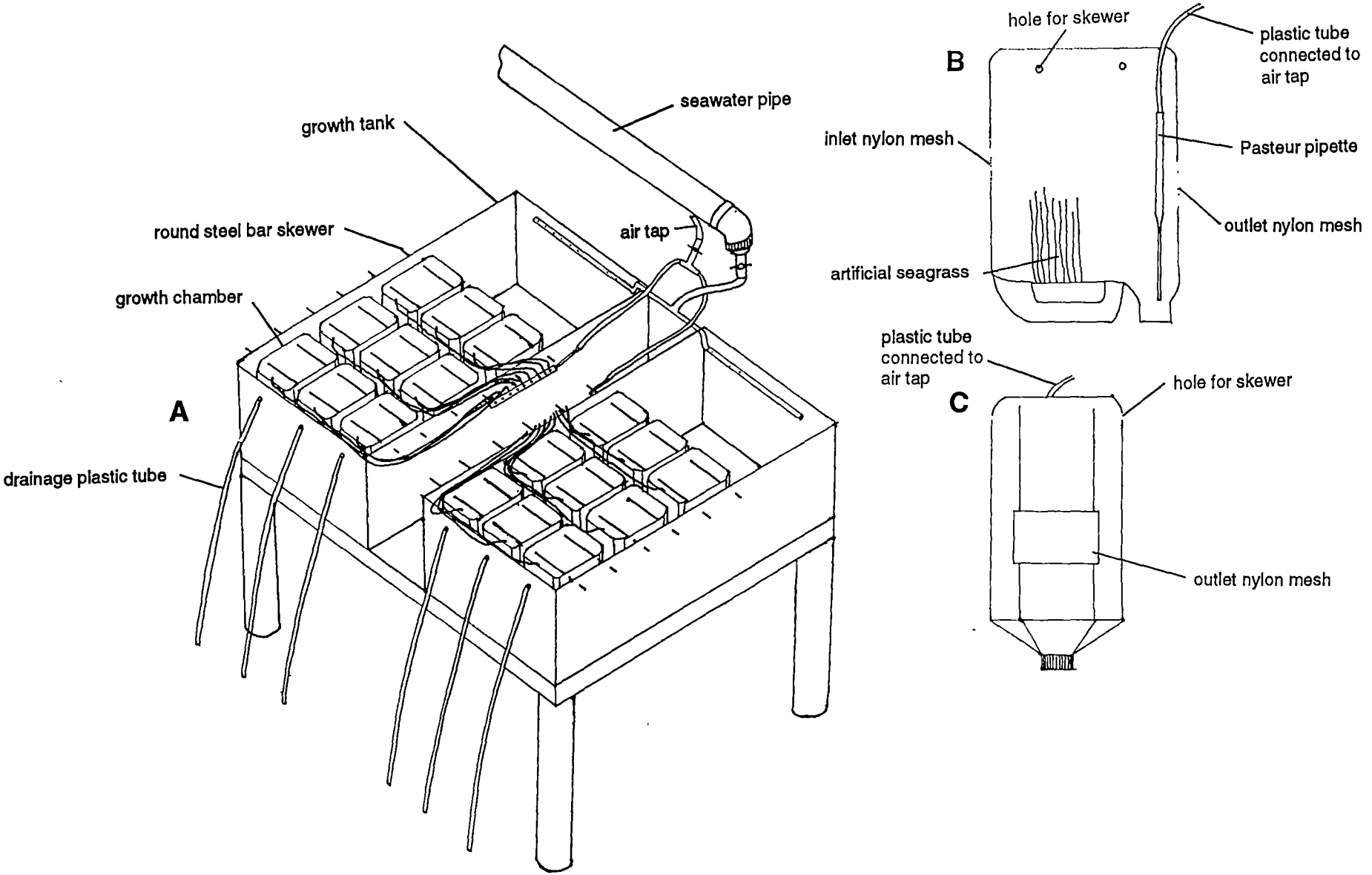


Figure 7.1 A. Set-up for the growth experiments. B. Lateral view of the inner right half of the growth chamber. C. Anterior view of the growth chamber. Not drawn to scale.

At seawater flow velocity of 10 cm s^{-1}, the volume of seawater inside each small chamber was fully replaced within 1.5 h as traced using fluorescein dye. The bottom of each of the 4-L plastic chambers directly below the outlet meshing had a 2 cm deep and 4 cm inner diameter depression which served to collect dead mysids and some of the uneaten food (Fig. 7.1B). A Pasteur pipette with the larger end attached to an aeration tap and the other smaller diameter pointing towards the bottom was vertically attached on the inner wall 1 cm above the bottom. Slowly released bubbles from the pipette generated mild turbulence and allowed mixing of the contents of each small chamber. A patch of artificial seagrass, made of 7 cm x 1 cm strips of plastic garbage bag glued onto a 16 cm^2 piece of sandpaper, was also attached on the bottom of the small tank to provide refuge and discourage cannibalism among mysids. The unidirectional flow of seawater was from the anterior of the large tank, through to the small chambers, and draining through three 2 cm inner diameter plastic tubes attached to the posterior side of the large tank (Fig. 7.1).

Design, Maintenance, and Duration of the Experiment, and Food Types

Autumn Experiments

The autumn experiment consisted of three mysid species held separately and fed with three types of food. A treatment comprised the three mysid species simultaneously fed with equal amounts of one of the three food types. Each treatment was replicated three times and included a control for each food type which consisted of unfed individuals. Twenty individuals of each species were placed in each culture chamber. Two large tanks each with nine 4-L chambers were set up allowing two types of food to be tested simultaneously.

The three food types comprised algal detritus, zooplankton and phytoplankton. The detritus was prepared by drying collected *Lessonia corrugata*, one of the locally abundant brown seaweeds, at 60°C for 2 days, grinding to < 63 μm particle size, and ageing in filtered seawater for 14 days (Roman 1984; Mullin and Roman 1986). The live zooplankton diet consisted of one to two day old *Artemia* sp. nauplii. Fresh

nauplii were obtained from daily hatches provided by the Finfish Development Program based at the Marine Laboratories where *Artemia* sp. cysts (Olympic®) are hatched in large quantities. Log phase of the phytoplankton *Isochrysis galbana* (Tahitian strain) was also obtained from the bulk cultures maintained by the Finfish Program. After daily siphoning out of uneaten food, dead mysids, and amorphous mysid exuviae, fresh food was also supplied daily *ad libitum*.

Survivorship curves for the treatment and control individuals were prepared for each mysid species. Mysids were allowed to grow for 15 days, during which the animals experienced ambient water temperatures which ranged from 14 to 17°C, ambient salinity of 34 to 35 ‰, and 12-h light and 12-h dark photoperiod. The experiment was concluded by removing the remaining mysids from their tanks. These animals were then anaesthetized, and their final body sizes measured by the same techniques utilized at the commencement of the trial.

Spring Experiments

The spring experiments examined (1) the effects of combining mysid species and feeding them with reduced density of *Artemia* sp. nauplii, and (2) the suitability of a larger and different species of phytoplankton on the growth of the three species. In the first experiment, either two (the two smaller species, *A. mixta australis* and *T. tasmaniae*) or all three species were held in the same growth chamber. Both the two- and three-species combinations were replicated three times. The food density of two to five live *Artemia* sp. nauplii mL^{-1} was supplied to the combined two-species chambers. The food density was doubled for the combined three-species chambers. Fresh one to two days old nauplii were supplied daily. The initial number of individuals was 18 for *A. mixta australis*, and 15 for *T. tasmaniae* for both two- and three- species chambers, and 20 for *P. rufa* in the three-species chambers.

All three mysid species were held separately in the 15-day experiment which used the larger phytoplankter (20-30 µm), the diatom *Phaeodactylum* sp as food. Excess amounts (1.32-2.36 x 10^6 cells mL^{-1}) of log phase *Phaeodactylum* sp. were supplied daily after removing clumps by coarse filtration using a 140 µm nylon sieve.

The water temperature during the autumn and spring experiments ranged from 14 to 17°C and 11 to 15°C, respectively. The salinity in both experiments varied between 33 and 34 ‰. In the combined species experiment, the two-species chambers were maintained for 20 days, five days more than in the autumn experiment. In the 3-species chambers, *A. mixta australis* and *T. tasmaniae* were first kept together for 10 days, then *P. rufa* was introduced. The former two species, were together in total for 25 days because the experiment had to complete a 15-day duration so that the growth rate of *P. rufa* could be compared to when this species was held alone in the autumn experiment.

Results

Survivorship in Control and Fed Mysids (Autumn Experiment)

Except for *T. tasmaniae*, the control individuals showed 100 % mortality in less than 8 days of being placed in the growth chambers (Fig. 7.2A,B). *Tenagomysis tasmaniae*, however, withstood starvation for up to 4 days, except in the third replicate which consisted of juvenile stages. This replicate followed similar patterns to those in the other two species (Fig. 7.2C). The first two replicates of *T. tasmaniae* and of *A. mixta australis* were early immature stages, whereas those of *P. rufa* were all juvenile stages. The first two replicates of *T. tasmaniae* reached 100% mortality by day 9 to 11 (Fig. 7.2C). In all three species, except the first two replicates of *T. tasmaniae*, 50% of individuals remained swimming in the growth chambers, 2-4 days after day 0. The other two replicates of *T. tasmaniae* individuals showed 50% mortality on days 7 and 10 (Fig. 7.2C).

Phytoplankton-fed individuals of *A. mixta australis* and *P. rufa* showed similar survivorship curves to that of the control (unfed) individuals in that 100% mortality occurred within 5 days (Fig. 7.3A,B). Phytoplankton-fed *T. tasmaniae* juveniles all died after 6-7 days (Fig. 7.3C). Fifty percent mortality in phytoplankton-fed *P. rufa* juveniles occurred in two days, while *A. mixta australis* survived only 1-3 days, but fifty

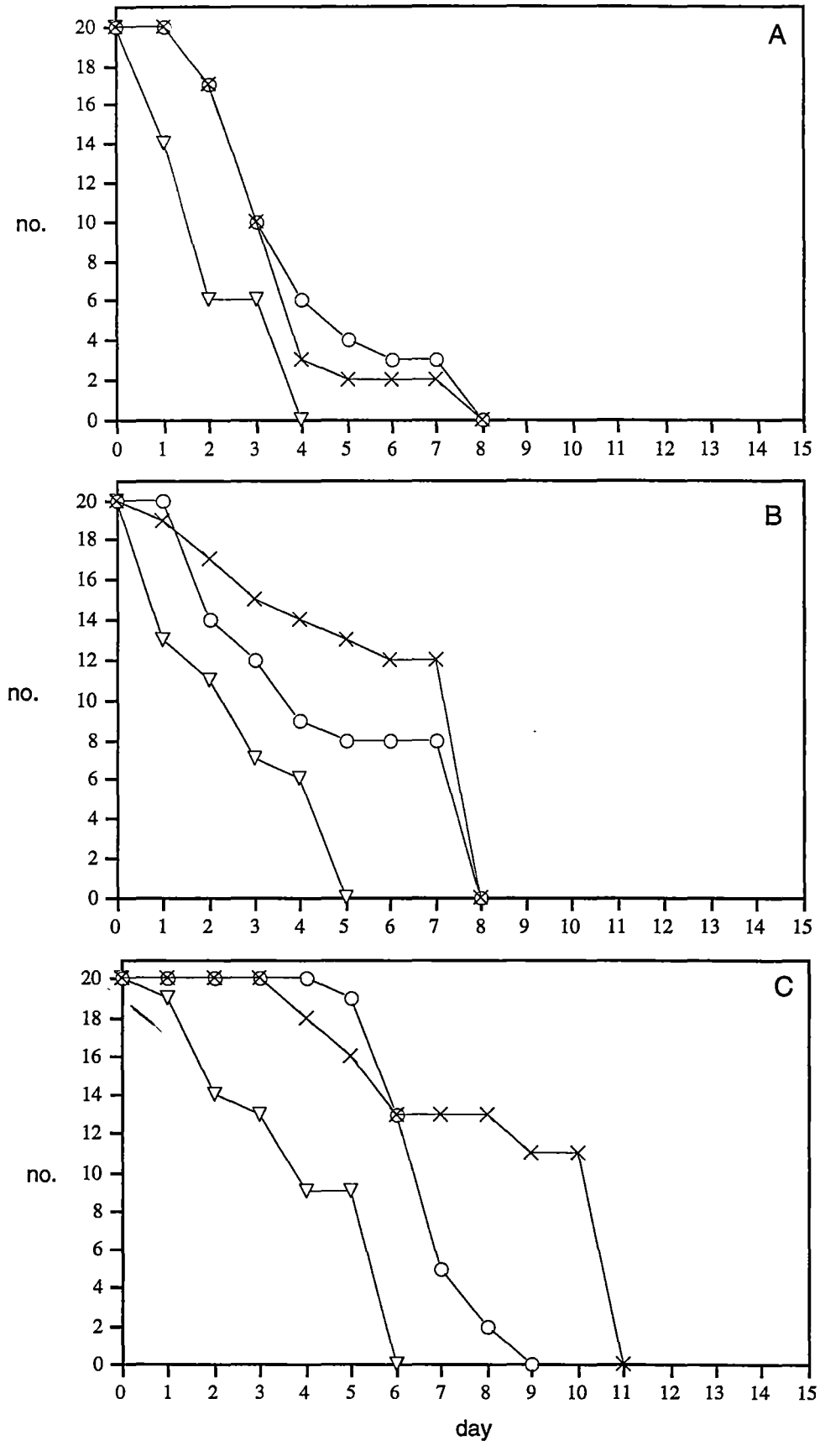


Figure 7.2 Survivorship curves of control (starved) mysid individuals. A. *Anisomysis mixta australis.* B. *Paramesopodopsis rufa.* C. *Tenagomysis tasmaniae.* Legend: cross - replicate 1, open circle - replicate 2, open triangle - replicate 3.

percent of the phytoplankton-fed *T. tasmaniae* remained alive on days 6 and 7. Algal detritus-fed *A. mixta australis* and *P. rufa* individuals showed 100% mortality from day 5 to 8 which was similar to the results for the unfed individuals. Again, like those in the control and those in the phytoplankton-fed individuals, 50% mortality of the population occurred on days 2-4. Algal-detritus-fed *T. tasmaniae* individuals did not attain 100% mortality; 3-8 individuals or 15 to 40% survived and grew on this diet up to the end of the experiment (Fig. 7.3C). Somatic growth of these individuals is described below. Fifty percent mortality occurred in all three replicates of *T. tasmaniae* on days 9 to 10.

Artemia sp. fed individuals of the three mysid species shared varying survival but did not reach 100% mortality in any replicate (Fig. 7.3A,B,C). The number of surviving *P. rufa* individuals on the *Artemia* sp. diet ranged from 8 to 11 (see Table 7.1) or 40 to 55% of the original population. Forty percent mortality in this species occurred on day 8. Fifty to ninety-five percent of the *Artemia* sp.-fed *T. tasmaniae* survived. Except for one replicate, 20 to 25% mortality of this species occurred on day 8. *A. mixta australis* showed the highest survivorship; 80 to 100% of the original number of mysids survived and grew up to the end of the experimental period.

Survivorship of Mysids in the Spring Experiments

The survivorship pattern shown by *Phaeodactylum* sp.-fed *A. mixta australis* is similar to the control (unfed) and those in the *Isochrysis* sp.-fed individuals (Fig. 7.4A). One hundred percent mortality of these individuals was reached on the 7th and 8th day. In the 2-species chambers, *A. mixta australis* showed 55.5% to 94.4% (10-17 individuals) survival after 25 d, but this decreased in the 3-species chambers with 38.8% to 50% (7-9 individuals).

Similar survivorship curves were shown by *Phaedactylum* sp.-fed *P. rufa* as those in the control and *Isochrysis* sp.-fed individuals (Figs. 7.3B, 7.4B). Mortality reached 100% on day 8 in two replicates and on day 11 in the third. Thirty to forty five percent (6-9 individuals) *P. rufa* survived in the 3-species chambers.

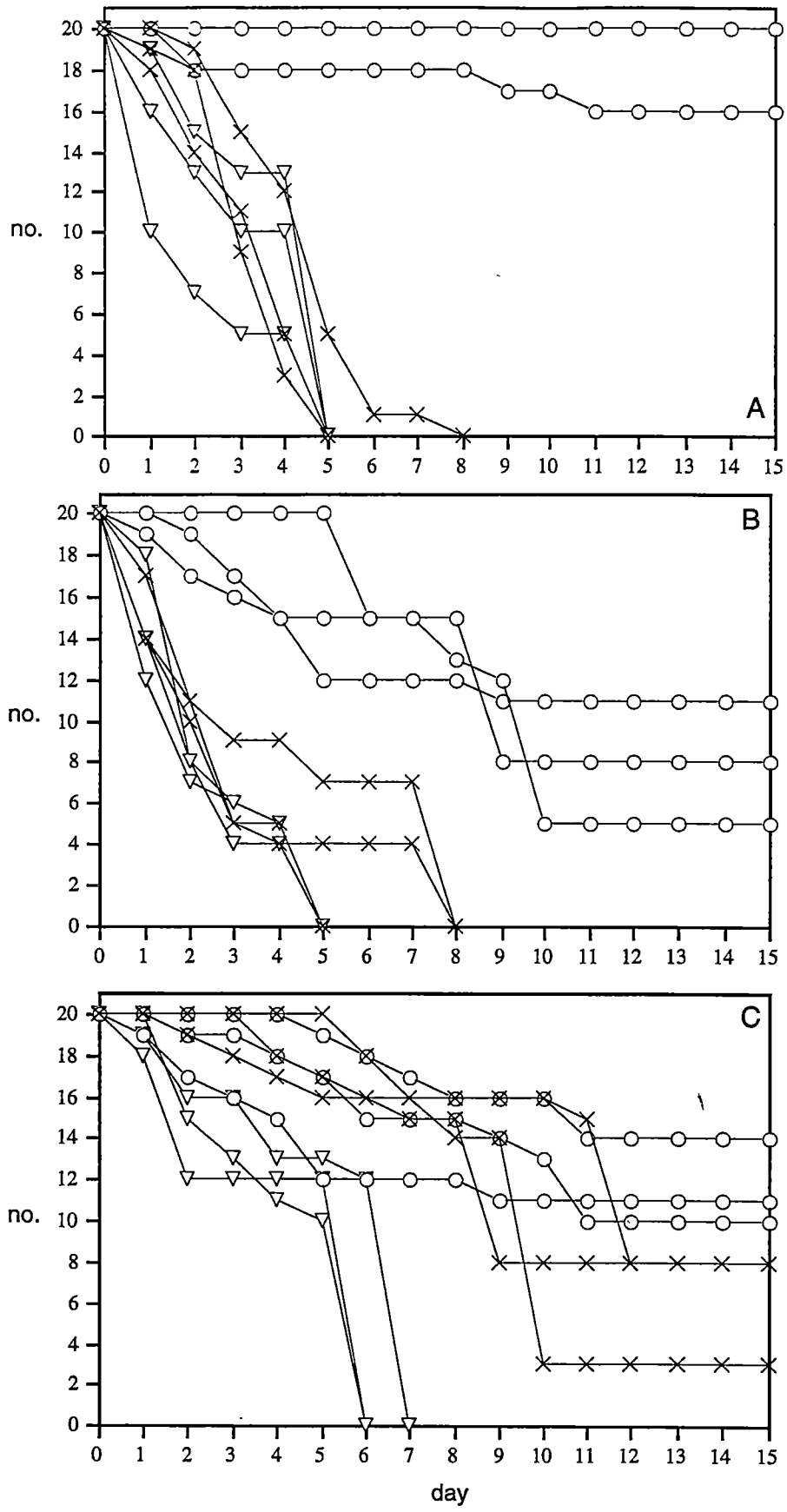


Figure 7.3 Survivorship curves of fed mysid individuals in the autumn experiment. A. *Anisomysis mixta australis.* B. *Paramesodopsis rufa.* C. *Tenagomysis tasmaniae.* Legend: cross - algal detritus, open circle - *Artemia* sp. nauplii, open triangle *Isochrysis galbana.*

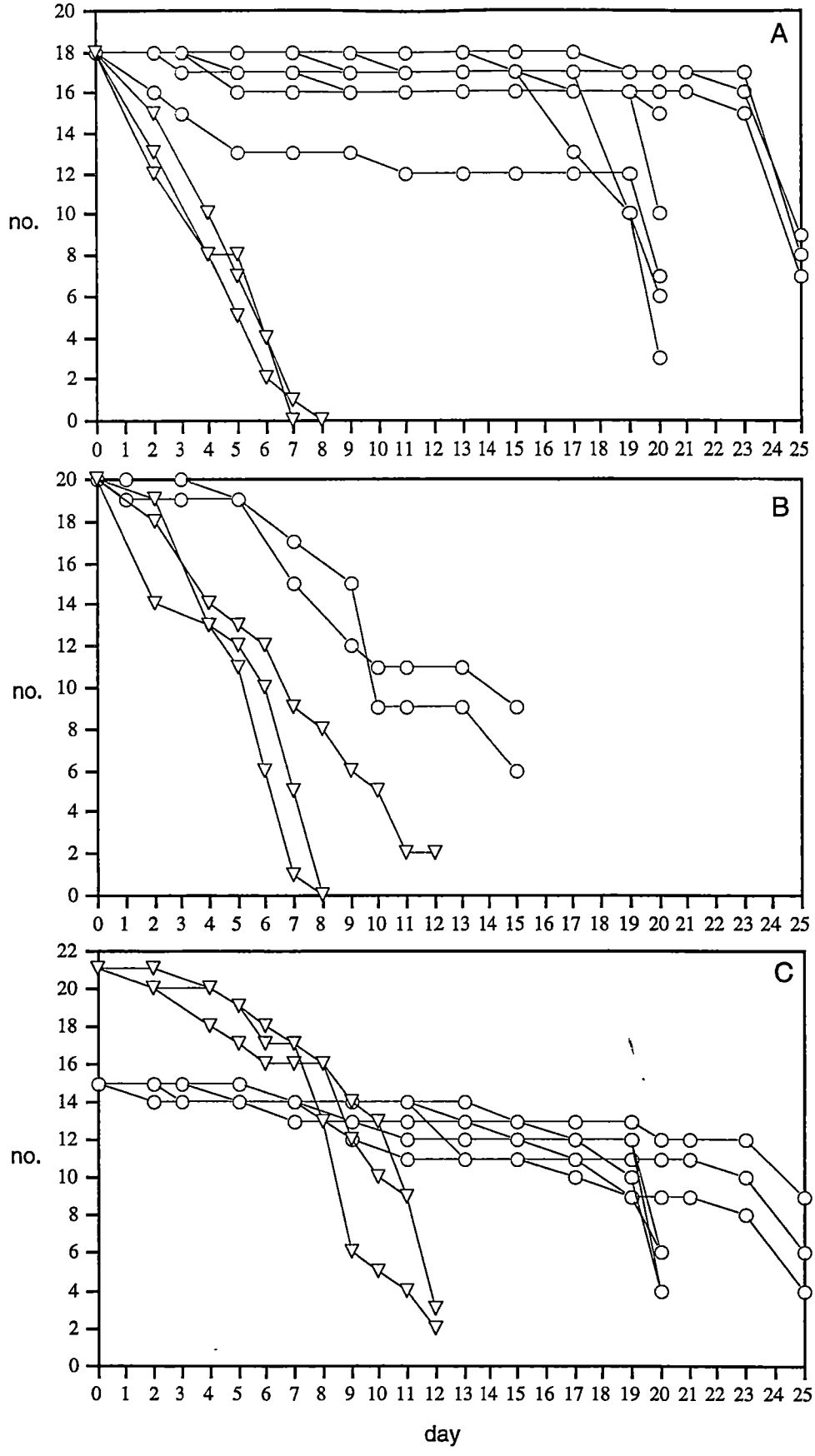


Figure 7.4 Survivorship curves of mysid individuals in the spring experiment. A. *Anisomysis mixta australis*, B. *Paramesopodopsis rufa*, C. *Tenagomysis tasmaniae*. Legend: open triangle - *Phaeodactylum* sp., open circle - *Artemia* sp. nauplii. *Phaeodactylum* sp.-fed individuals were held separately, while the nauplii-feed ones were held either as 2-species (*A. mixta australis* and *T. tasmaniae*) or 3-species.

The survivorship curves of *T. tasmaniae* fed with *Phaeodactylum* sp. differ markedly from those of *Isochrysis*-fed individuals because the former group did not reach 100% mortality on day 8, and a few (2-3) individuals (9.5% to 14.3%) were alive at the end of the experiment (Fig. 7.4C). Thirty three to forty percent (5-6 individuals) *T. tasmaniae* individuals survived after 20 days coexisting with *A. mixta australis*. These values are comparable with the 26.6% to 46.6% (4-7 individuals) survival in the 3-species combination.

Somatic Growth and Growth Rate in the Autumn Experiment

Table 7.1 Increase in body length (G in mm), body length growth rate (GR in mm day^{-1}) and percentage growth from initial size in three mysid species fed with three different diets. Single mysid species per chamber

	Paramesopodopsis rufa			*Tenagomysis tasmaniae*			*Anisomysis mixta australis*		
	G	GR	%	G	GR	%	G	GR	%
Diet (rep. no.)									
zooplankton									
(1)	1.470 (n=8)	0.098	69.0	0.710 (n=10)	0.047	19.9	1.380 (n=16)	0.092	57.2
(2)	1.050 (n=5)	0.070	50.2	0.850 (n=14)	0.056	23.5	1.540 (n=20)	0.102	58.7
(3)	1.590 (n=11)	0.110	72.3	1.350 (n=19)	0.090	85.9	1.240 (n=20)	0.080	86.1
Seaweed Detritus									
(1)	–	–	–	0.190 (n=3)	0.012	5.1	–	–	–
(2)	–	–	–	0.630 (n=8)	0.042	19.6	–	–	–
(3)	–	–	–	0.770 (n=8)	0.050	50.6	–	–	–
small phytoplankton (flagellate) *Isochrysis galbana*									
(1)	–	–	–	–	–	–	–	–	–
(2)	–	–	–	–	–	–	–	–	–
(3)	–	–	–	–	–	–	–	–	–

Table 7.1 shows somatic growth, daily growth rate, and percent growth from the initial size of individuals which survived and grew up to the end of the autumn experiment. All three species fed with *Artemia* sp. nauplii showed similar daily growth rates (Kruskal-Wallis test, $H = 3.29$, df = 2, $p < 0.05$).

Somatic growth of *Artemia* sp.-fed *A. mixta australis* ranged from 1.24 to 1.54 mm or a daily growth rate range of 0.080 to 0.102 mm. Individuals of this species grew 57.2% to 86.1% of their initial sizes.

Artemia sp.-fed *P. rufa* showed an increase in body size ranging from 1.05 to 1.59 mm, which is equivalent to a daily growth range of 0.07 to 0.11 mm. These individuals grew 50.2% to 72.3% of their initial body sizes.

T. tasmaniae individuals fed with algal detritus showed an increase in body size of 0.190 to 0.770 mm which is equivalent to 0.012 to 0.050 mm per day. These individuals grew 5.1% to 50.3% of their initial body size over the 15-day experimental period. *Artemia* sp.-fed *T. tasmaniae* also showed a wide range of growth from 0.71 to 1.35 mm equivalent to a daily growth rate range of 0.047 to 0.090 mm. The same individuals grew 19.9% to 85.9% of their initial body sizes. Similar daily growth rates were shown by *T. tasmaniae* individuals fed with the two types of food (Mann-Whitney test, $U = 8$, df = 1, $p > 0.05$).

Somatic Growth and Growth Rate of Mysids in the Spring Experiment

Results in the spring experiment are shown in Table 7.2. Daily growth rates of the three species combined were significantly different (Kruskal-Wallis test, $H = 6.25$, df = 2, $p < 0.05$) with *P. rufa* having higher growth rates than the other two species (non-parametric Tukey-type test, $p < 0.05$ for all). The variations were also explained by the higher daily growth rates of *A. mixta australis* than those in *T. tasmaniae* (non-parametric Tukey-type test, $p < 0.001$). In the two species combination, the daily growth rates of both species were comparable (Mann-Whitney test, $U = 8.5$, df =1, $p > 0.05$).

Table 7.2 Increase in body length (G in mm), body length growth rate (GR in mm day^{-1}) and percentage growth from initial size in the three mysid species in the combined and *Phaodactylum* sp. feeding experiments.

	Paramesopodopsis rufa			*Tenagomysis tasmaniae*			*Anisomysis mixta australis*		
	G	GR	%	G	GR	%	G	GR	%
Diet (rep. no.)									
large phytoplankton (diatom) *Phaeodactylum* sp.									
(single species per chamber)									
(1)	–	–	–	0.425 (n=3)	0.040	21.3	–	–	–
(2)	–	–	–	0.536 (n=2)	0.045	26.4	–	–	–
(3)	–	–	–	0.440 (n=3)	0.037	21.6	–	–	–
zooplankton									
(2-species combination)									
(1)				0.920 (n=5)	0.046	54.9	1.023 (n=10)	0.051	72.5
(2)				0.855 (n=6)	0.043	49.9	0.924 (n=17)	0.046	63.3
(3)				0.853 (n=6)	0.043	50.8	1.066 (n=15)	0.053	75.6
(3-species combination)									
(1)	1.278 (n=9)	0.085	46.5	1.601 (n=7)	0.064	56.2	1.458 (n=8)	0.058	105.1
(2)	–	–	–	1.616 (n=7)	0.065	53.9	1.351 (n=7)	0.054	95.3
(3)	1.174 (n=6)	0.078	43.8	1.832 (n=4)	0.073	59.7	1.542 (n=9)	0.062	110.9

A. mixta australis in the 2-species chamber grew 0.924 to 1.066 mm, and the converted daily growth ranged from 0.046 to 0.053 mm. Increase in the body lengths of *A. mixta australis* in the 2-species chambers range from 63.3% to 75.6% . In the 3-species combination the somatic growth for *A. mixta australis* ranged from 1.351 to 1.542 mm, which is equivalent to an increase ranging from 95.3% to 110.9% of the initial sizes. Their daily growth rate range of 0.054 to 0.062 mm was comparable to that when they were mixed with *T. tasmaniae* (2-species combination) (Mann-Whitney

test, $U = 8.5$, df = 1, $p > 0.05$). However, pooled growth rates of *A. mixta australis* from both two- and three-species combinations were 50% slower than those rates when they were held alone (Mann-Whitney test, $U = 18$, df = 1, $p < 0.05$).

The somatic growth of *P. rufa* in the 3-species chambers ranged from 1.174 to 1.278 mm, while its growth rate ranged from 0.078 to 0.085 mm day^{-1}. The percentage increase in its body length varied from 43.89% to 46.5%. Its high daily growth rates are comparable to those when it was held separately from the other two species (Mann-Whitney test, $U = 4$, df = 1, $p >> 0.05$).

T. tasmaniae somatic growth in the 2-species chambers ranged from 0.853 to 0.920 mm. Its growth rate range of 0.043 to 0.046 mm day^{-1} is comparable to its growth when held separately from the other two species (Mann-Whitney test, $U = 12$, df = 1, $p >> 0.05$). In the 3-species combination, *T. tasmaniae* increased its body length by 1.601 to 1.832 mm, equivalent to 56.2% to 59.7% of initial sizes. Its growth rate of 0.064 to 0.073 mm day^{-1} is higher than those in the two-species chambers (Mann-Whitney test, $U = 19$, $p < 0.05$).

The somatic growth of *T. tasmaniae* individuals which survived on *Phaedactylum* sp. diet ranged from 0.425 to 0.536 mm for the 12 day duration. This increase in body length is equivalent to 21.3% to 26.4% increase from the initial size. Daily growth rates of *T. tasmaniae* individuals fed with *Phaeodactylum* sp. and seaweed detritus (autumn experiment) were comparable (Mann-Whitney test, $U = 5$, df = 1, $p > 0.05$).

Discussion

Cold and warm temperate mysid species which experience varying seasons and temperature regimes show highly plastic growth patterns, in particular in attaining age and size at sexual maturity (Mauchline 1985). Young released during spring grow faster and reach sexual maturity quicker than those young released during colder months. Asthorsson and Ralph (1984) noted that in *Neomysis mercedis*, both summer- and winter-released juveniles show similar growth rates, but inter-moult

periods are much abbreviated in the individuals released in warmer months. This suggests that summer released young attain sexual maturity at a smaller size than those released during colder times. High levels of high quality food (protein based) during warmer months are being consumed at higher rates by the warmer-released young (Mauchline 1985; Rudstam 1989).

Growth rates obtained in the present study from the three co-existing species are comparable to those reported in cold and warm temperate mysid species of the northern hemisphere (Mauchline 1980,1985). For instance, laboratory reared juvenile stages of *Neomysis integer* which were fed with *Artemia* sp. nauplii had a daily average growth of 0.06 mm at 9°C and 0.09 mm at 16°C (Asthorsson and Ralph 1984). Field estimates of the growth rates showed that juveniles released during summer grew at a rate of 4 to 5 mm monthly while the winter generation had a growth rate of 3 to 4 mm. Juveniles of *Mysis gaspensis* have been estimated to grow 3 mm in body length in 19 days and at habitat temperature of 17-18°C (Dadswell 1975). From analysis of field samples, Fenton (1986) estimated the growth rates of the juveniles of the three species used in the present experiments to be similar. *Tenagomysis tasmaniae* juvenile stages showed a monthly growth rate of 2.15 mm (0.069 mm day^{-1}), while *A. mixta australis* and *P. rufa* juvenile stages grew at 2.02 mm per month (0.065 mm day^{-1}). In the autumn experiment, except for the first two replicates of *T. tasmaniae* which grew at rates similar to Fenton's (1986) estimates, the other *T. tasmaniae* replicate and those in the other two species appeared to exceed the growth rates estimated by Fenton. Laboratory conditions with high levels of protein-based food may explain this disagreement.

Results from both autumn (mysid species held separately) and spring (2- and 3-species combination) experiments all suggest that the three species have similar potential to grow on similar food, *i.e. Artemia* sp. nauplii. Lower average temperature in the early spring (13°C ± 1.58) than in the autumn (15.5°C ± 1.29) experiment may explain the faster growth rates in both *T. tasmaniae* and *A. mixta australis*. However, because these temperature ranges experienced by the three species in both experiments are fairly similar, the importance of the concentration of food which supports growth in the three mysid

species may exert a dominant influence. This seems to be the case for *A. mixta australis* and *T. tasmaniae*, both of which showed faster daily growth rates with excess amounts of nauplii in the autumn experiment than those experiencing reduced food in the spring experiment. Response to increased level of food is also evident in the spring experiment. *T. tasmaniae* grew at faster rates with the food level doubled when three species were held together than those in the two-species combination. Although a slight increase in growth was shown by *A. mixta australis* when held in combination with the other species, the rates however, were not significantly different. The interesting aspect of these results is the similar high growth rates of *P. rufa* in both autumn and spring experiments. This may clearly indicate that this species is highly efficient at feeding on the animal food type, and that it can sustain growth rates regardless of the difference in food levels used in the present study. *P. rufa*'s performance further indicates that these food levels were well above the critical threshold of food concentration. These results appears to lend support to the theory that growth in mysids may be food rather than temperature limited (Hansson *et al.* 1990), at least at the range of temperature over which these experiments were conducted.

Distribution of these animals in the field shows a vertical stratification (Fenton 1992), with *T. tasmaniae* adopting a close association with the substrate and probably feeding on large amounts of algal detritus, in contrast to the primarily pelagic *P. rufa* and *A. mixta australis*. *Tenagomysis tasmaniae* appears to differ from the other two in its ability to utilize seaweed detritus. The mechanism of algal detritus utilization by this species is an interesting subject for further investigation, in particular the possibility of a capability to digest this material either by facultative or obligate microbial organisms (Wainwright and Mann 1982) or by production of endogenous enzymes (Friesen *et al.* 1986), or even both.

Despite being offered at high concentrations, the phytoplankton *Isochrysis galbana* did not support growth let alone survival in all three species. This result strengthens the conclusion of Mullin and Roman (1986) that the phytoplankter *Isochrysis* sp. is not a suitable food for mysids. The small size of *I. galbana* may explain its

unsuitability. However, results using the larger size diatom, *Phaedactylum* sp. not only confirm the fact that phytoplankton is not an appropriate food type for *A. mixta australis* and *P. rufa*, but also provide evidence that *T. tasmaniae* is able to assimilate this food type. Feeding on phytoplankton has been reported in other mysid species (*e.g.* Pechén-Finenko and Pavlovskaya 1975; Mauchline 1980; Grossnickle 1982; Webb *et al.* 1987, 1988). A mixture of other larger size, chain-forming, and locally isolated phytoplankton species needs to be tested as food for the three mysid species in future studies.

It is surprising that *P. rufa* and *A. mixta australis* did not utilize algal detritus for growth, and both showed poor survivorship on this food type. This food type was included in the present study because Mullin and Roman (1986) noted that mysids may also ingest algal detritus apart from ingesting primarily animal food. In addition, algal detritus has been regarded as a component in the diet of the three species as revealed by the gut content analysis (Fenton 1986). In chapter 5 the three species ingested algal detritus though at very low rates. Perhaps the levels of allelochemicals in the aged algal detritus were still intolerable for the two species, but not for *T. tasmaniae*. This is very likely since algal detritus-fed *P. rufa* and *A. mixta australis* died earlier than the starved controls of the two mysid species. The unsuitability of algal detritus for growth of estuarine organisms as has been noted in many studies (*e.g.* Kirby-Smith 1976; McTigue and Zimmerman 1991) is further supported by the present results for *P. rufa* and *A. mixta australis*. In contrast, algal detritus has been regarded as a food supplement which may be utilized for growth when the most preferred food is scarce (Roman 1984; Stuart *et al.* 1985; Paffenhøffer and van Sant 1985). This ambiguity of the role of algal detritus points to the fact that it is still very difficult to reproduce in the laboratory the optimal quality of this abundant potential food in the marine environment (Kirby-Smith 1976; Mann 1988).

It is interesting to note that the smallest species, *A. mixta australis*, showed the best results with a survival of 80-100%, and growth rates similar to those of larger species. The foregut morphology of this species (see chapter 8) is best adapted to fine particulate matter though from the present study, it copes effectively with soft and

larger particulate food as represented by *Artemia* sp. nauplii. In the field, the ability to utilize similar live animal food would suggest strong exploitative competition with the mainly pelagic *P. rufa*, but because both differ in size the two species are expected to partition food resource by predation on different prey size. The larger species, *P.rufa*, may tend to eat larger sizes of prey. *A. mixta australis* has a cosmopolitan geographical distribution (Fenton 1986). By virtue of its relatively small size and probably being eurytopic, this species may act as an opportunistic or fugitive species, and might occupy the vacant feeding niche in between the two divergent endemic *P. rufa* and *T. tasmaniae* species.

Despite the wide phylogenetic difference, results of studies of natantian decapods may shed light on feeding habits of mysids because these groups show similar general form and behaviour (Mauchline 1985). Laboratory growth experiments on two co-existing saltmarsh prawns revealed similar growth rates on the combined diets of animal (*Artemia* sp nauplii) and plant (*Skeletonema* sp.) materials (McTigue and Zimmerman 1991). The white shrimp, *Penaeus setiferus* could utilize the plant food for growth up to a certain number of days only. *P. aztecus*, the brown shrimp, had been reported earlier (Gleason and Zimmerman 1984) to use both types of plant food (benthic diatoms and *Spartina* detritus). However, McTigue and Zimmerman (1991) noted that this species may depend solely on animal food for growth. The latter authors speculated that the two species evolved a divergence of feeding habits in response to competition for food, and that these shrimps thus partition food resources by differences in life history strategies and habitat utilization relative to the availability of food resource at the time of immigration. The brown shimp, *P. aztecus*, occupies the habitat during high abundance of benthic animals which are extensively fed on by this species, and *P. aztecus* grows much faster than the white shrimp. *P. setiferus* colonizes the habitat later gleaning the remaining benthic animals and feeds on benthic diatoms and the epiphytes of *Spartina*.

Clutter (1967) hypothesized that if co-existing mysid species grown in similar food conditions show similar growth rates then in the field they are highly likely to compete for the same limiting food resource. In the present study, the fact that the

three species showed very similar growth rates in conditions where they were held separately and fed in excess with animal food, suggests some competitive release or some degree of expansion in their fundamental feeding niche, assuming they are indeed competing in the field. The slight growth of *T. tasmaniae* feeding on the algal detritus, and its ability to grow at a comparable rate when feeding on the diatom, *Phaeodactylum* sp. as when eating animal food, indicates that this species has a much broader feeding niche compared with the other two species.

CHAPTER 8

MORPHOLOGY OF THE CEPHALOTHORACIC FEEDING APPENDAGES AND FOREGUT

Introduction

According to the *Bauplån* (the German word for "a structural design") concept, invertebrates are constrained by their structural plans particularly in their functioning, behaviour, and overall interaction with the environment (Brusca and Brusca 1990). These sets of body plans have allowed invertebrates to exploit almost all types of habitats and the food items present in those habitats. For instance, the feeding mechanisms of invertebrates vary considerably particularly in capture and digestion (Levinton 1982; Barnes *et al.* 1988). The competition theory assumes that competition influences phenotypic variations in organisms during their evolution (Schoener 1974, 1982, 1989). Therefore, the *Bauplåne* of invertebrates may be perceived as a consequence of competition. Although similarities of basic and/or gross structures could be expected, subtle morphological differences would also be apparent particularly among competing species that require a very similar range of food types, and are found in similar habitats. As a means of alleviating competition, the feeding niche dimension may be partitioned by obvious and slight differences in feeding structures and associated feeding mechanisms (Schoener 1974; Caine 1974, 1977; Wagner and Blinn 1987).

Studies of mysid diets by gut content analysis have generally revealed a broadly omnivorous feeding habit (reviewed in chapter 1), however with tendencies toward carnivory, herbivory and/or detritivory (*e.g.* Nath & Pillai 1973; Siegfried and Kopache 1980; Mauchline 1980; Wooldridge and Bailey 1982; Zagursky and Feller 1985; Webb and Wooldridge 1989). In addition to qualitative accounts of food items by gut content analysis, morphological investigation of feeding apparatus is required to fully understand feeding habits and ecology of organisms (Anraku and Omori 1969; Kunze and Anderson 1979; Webb and Wooldridge 1989; Ohtsuka and Onbe 1991).

Webb and Wooldridge (1989) noted the strong relationship between mouthparts, foregut morphology, and the feeding habits of two co-occurring mysids.

Information from studies dealing with single species cannot readily be applied to other mysid species (Cannon and Manton 1927; Crouau 1987, 1989; Mauchline 1980). As in the case for marine amphipods (Caine 1977) and in copepods (Vanderploeg 1990), feeding morphology and behaviour of the group are not expressed in any single species because different species most likely reflect a diversity of feeding mechanisms and feeding structures. A comprehensive comparative study is required to determine their functional significance (Mauchline 1980).

The Structure of Cephalothoracic Feeding Appendages

Mysids were previously thought to be the closest relatives of euphausiids (the two previously belonged to the same Order Schizopoda), but have now been separated with mysids belonging to Peracarida and euphausiids to the Eucarida. However, mysids show a similar form of feeding appendages with those in euphausiids (Mauchline 1980). One major difference between these groups is that setules and microsetules on the setae on most mysid thoracic endopods are not as elaborate as in euphausiids. In *Mysis relicta*, the setae on the endopods have been suggested to increase efficiency of these appendages in grasping and manipulating large prey (Sierszen *et al.* 1982). The majority of setae with elaborate setulations are found on the mouthparts of mysids. These setae are similar to those in copepods (Tiselius and Jonsson 1990) with setules concentrated on the base of each seta. This has led previous investigators to conclude that most processing of fine particles may only be occurring in the mouthparts, in particular the first and second maxillipeds (first and second endopods *sensu* Tattersall and Tattersall 1951), maxillae, maxillules, the labial paragnaths, labrum and the mandibular palps (Mauchline 1980; Crouau 1989).

The potential size range of food particles that may be captured by suspension feeding crustaceans may be predicted from the intersetal and intersetular gap measurements. This has been demonstrated in calanoid copepods which utilize their

bristled second maxilla in capturing suspended food particles (Boyd 1976). A similar approach has been useful in elucidating the potential sizes of food particles that can be captured by the thoracic appendages of euphausiids (McClatchie and Boyd 1983; Hamner 1988; Mauchline 1989). The microsetular gaps which can be as fine as 1 to 2 μm in euphausiids indicate efficiency at capturing nanoplanktonic cells (McClatchie and Boyd 1983; Dalley and McClatchie 1989). Webb and Wooldridge (1989) observed a marked difference in intersetular gap ranges in two co-occurring mysid species which differ in diet.

A close relationship between feeding types and the dentition of the mandible has been shown in calanoid copepods (Anraku and Omori 1963; Itoh 1970; Sullivan *et al.* 1975; Schnack 1989; Ohtsuka and Onbe 1991). These studies have shown that the herbivorous species have mandibles with cutting edges provided with grinding teeth, the predatory species possess very sharp teeth, and the omnivorous species possess mandibular dentition intermediate between the other feeding types, *i.e.* the teeth are heavier than those of the herbivores, but they are not as stout as for predators. The face of the mandibles of mysids and euphausiids show almost identical characteristics except that the spine row and the *lacinia mobilis* are lacking in most adults of the latter and in some lophogastrid mysids (Mauchline 1980). Using scanning electron microscopy, McClatchie and Boyd (1983) examined, the fine structure of the *pars molaris* of *Euphausia superba*. Mauchline (1980) noted that herbivorous feeding in euphausiids is correlated with a large *pars molaris*, and highly predatory with small. This relationship has been demonstrated in some mysids (Mauchline 1980). In contrast to the well studied Order Euphausiacea, the mouthparts of the more diverse Mysidacea are little studied (Mauchline 1980; Crouau 1989).

The Structure of the Foregut

There have been few studies relating to the functional morphology of mysid foreguts (Gelderd 1909; Haffer 1965; Nath and Pillai 1973; Mauchline 1980; Friesen *et al.* 1986; Webb and Wooldridge 1989; Storch 1989). With the exception of the

latter two studies, qualitative descriptions and characterization of the different internal foregut structures have been primarily based on light microscopy. These studies may misinterpret the internal arrangement, topography, and three-dimensional orientation of the internal armature of the foregut, mainly due to problems with depth of field (Grice and Lawson 1971).

Specialization in terms of detailed form and armature of the stomach occurs between species. Light microscopy reveals well-developed spines, bristles, teeth, and stiff setae in the stomachs of burrowing littoral species, *e.g. Gastrosaccus simulans* (Nath and Pillai 1973). This species gets food mainly through seizing large food masses as shown in its cannibalistic habit of attacking disabled or dying companions, feeding on pieces of flesh of the chaetognath *Sagitta*, and other animals like crabs and mussels. Similar heavy chitinous teeth and thick barbed spines have been found in the cardiac stomach of *Mysis stenolepis* (Friesen *et al.* 1986). According to these authors, the foreguts of this mysid species are well adapted for masticating large food particles of plant and animal origin. In contrast, the strictly filter feeding subterranean freshwater species, *Spelaeomysis*, has a reduced cardiac stomach with neither strong spines nor teeth (Nath and Pillai 1973). Oshel & Steele (1988), from SEM observations, briefly described some foregut features of *Gnathophausia ingens*. In a comparative study, using the techniques of transmission and scanning electron microscopy, Storch (1989) described in detail the different food chambers and channels, cuticular ridges, and ultrastructure of the epithelial and cuticular linings of the foreguts of the nearshore mysids *Bowmaniella floridana*, *Mysidopsis bahia*, and *Praunus flexuosus*.

Aim of the Study

In the present study, scanning electron (SEM) and light microscopy were used to describe and compare the morphology of the thoracic endopods, mouthparts and the foregut internal armature of three Tasmanian mysid species. Feeding specializations

which may explain food resource partitioning and co-occurrence of these mysid species are examined in detail.

Materials and Methods

Mysid Field Collection and Laboratory Maintenance

The collection and laboratory maintenance of the three mysid species used in the present study are described in chapter 2.

General Morphological Methods

Adult individuals were cold narcotised before dissections of feeding structures under a binocular dissecting microscope. Mouthparts and stomachs for SEM and whole animals for serial sectioning were fixed for two hours in a solution of 2.5% glutaraldehyde, 0.2M phosphate buffer (pH = 7.3), and 0.14M NaCl. Fixed specimens were each washed three times for 10 minutes each with phosphate buffer followed by post-fixation in 2% osmium tetroxide in 1.25% sodium bicarbonate (pH = 7.2) for two hours. Tissues were washed as before, and rinsed with distilled water. Specimens were then dehydrated by placing them in an ascending series of ethanol concentrations (10 min in each from 10%-100% alcohol).

Specimens for scanning electron microscopy were immersed in 100% hexamethyldisilazane (HMDS, Sigma Chem. Co.) for 10 to 15 min, and air dried overnight at room temperature (Nation 1983). HMDS has proven to be effective in the highly chitinous foreguts of mysids without the use of critical point drying. However, mouthparts had to be critical point dried as tissue shrinkage occurred with HMDS treatment. Prior to examination, tissues were mounted on aluminium stubs, sputter coated with gold, and examined at an accelerating voltage of 15 kV in a Philips 501 SEM. For light microscopy, alcohol dehydrated specimens were each washed three times for ten minutes in 100% propylene oxide. Tissues were then embedded in epoxy

resin. Line drawings were prepared from serial semi-thin (1 μm) sections using a camera lucida fitted to an Olympus compound microscope. Semi-thin sections were stained with toluidine blue (Storch 1989).

Mouthparts for line drawing were dissected from individuals which were fixed in 5% neutral formalin in seawater. Dissected mouthparts were mounted on glass slides with cover slips using polyvinyl lactophenol as mountant, and drawn using a camera lucida attached to a microscope. Four pairs of mandibles from adult individuals of each species were examined to detect morphological differences among the three species. The edge index expressed as a ratio of the *pars molaris* longest length to the *pars incisiva* length (Nemoto 1977) was calculated for each species. Intersetal and intersetular distances of the mouthparts were measured from scanning electron micrographs.

Intersetal gap measurements were made from the 5 most anterior thoracic endopods of formalin preserved (5% v/v) individuals. The sixth or most posterior endopod was excluded because it mainly functions in grooming reproductive structures (see chapter 3). After measuring the total lengths of four specimens from each species, the intact right side endopods were dissected out and mounted in between glass slides and cover slips with polyvinyl lactophenol. Soon after mounting, the gaps were measured using a phase contrast compound microscope with an ocular micrometer. All intersetal gap measurements from the five endopods were pooled, and frequency and cumulative frequency distribution plots were constructed.

Foregut capacities may indicate feeding habits as reported for other peracarids (Jones 1968; Sheader and Evans 1975), and euphausiids (Nemoto 1977). To test this hypothesis, the gut capacity of the three mysid species adults were compared using the foregut index (FGI = LC x 100 /LV , where LC is the length of cardiac region, and LV, the length of the ventral plate from the cardiac region to the pyloric region) used by Suh and Nemoto (1988). In addition, the formula of a prolate spheroid which best approximates the shape of the mysid foregut filled with food, $4/3\ \pi\ a^2b$ (where a is one half the average of the stomach width and height, and b is one half the stomach length), was calculated for each dissected foregut to estimate volume (Murtaugh

1984). Mysids used in the FGI and gut volume calculations had previously been fed with a mixture of finely ground oven-dried (60°C) macroalgae and powdered fish pellets until their stomachs were full. Total lengths (tip of carapace rostrum to tip of telson) of fifteen heat-killed individuals of each species were measured, and their foreguts dissected out to estimate FGI and gut volume.

Results

The Structure of the Cephalothoracic Feeding Appendages

Basic Structure of the Thoracic Endopods and Mouthparts

The terminology used here is based on Mauchline's (1980) review. The description is from posterior to anterior feeding appendages.

Similar in gross form, the endopods show the basic set of podomeres or segments from proximal to distal: basis, pre-ischium, ischium, merus, carpus, propodus and dactylus (Fig. 8.1). Terminating in an enlarged nail, the three distal segments possess structures associated with the cleaning mechanism (Fig. 8.7E). The majority of setae project from the medial surface of these endopods (Figs. 8.1, 8.6B).

Although maxilliped II has a similar disposition and curvature (it overlies the ventral face of maxilliped I), the relatively longer length of the merus gives the fused carpo-propodus, and dactylus a more anterior position than the equivalent segments of maxilliped I (Figs. 8.2, 8.6A, 8.8A). Maxilliped I shows a similar gross form and is also composed of the basic podomeres (Fig. 8.3). Unlike in the thoracic endopods, these segments are wider and flatter due to the presence of lobes and flat endites. Along with the other mouthparts the pair of maxillipeds I form acute angles with the underside of the thorax (Figs. 8.3; 8.6A,D; 8.7A; 8.8A). The first maxillipeds form a ventral cover of the paired maxillae and maxillules.

The gross form of the paired maxillae is similar (Figs. 8.4, 8.7A, 8.8B). The maxillae are composed of concave thin plates which are in direct contact with the anterior surfaces of the first maxillipeds. Their setae-fringed exite projects outtowards

Figure 8.1 The second thoracic endopods of the three mysid species. a. *Anisomysis mixta australis*: ba - basis, pi - pre-ischium, is - ischium, me - merus, ca - carpus, pr - propodus, da - dactylus, n - nail. b. *Paramesopodopsis rufa* (abbreviations as in a). c. *Tenagomysis tasmaniae* (abbreviations as in a). Scale bars = 0.2 mm.

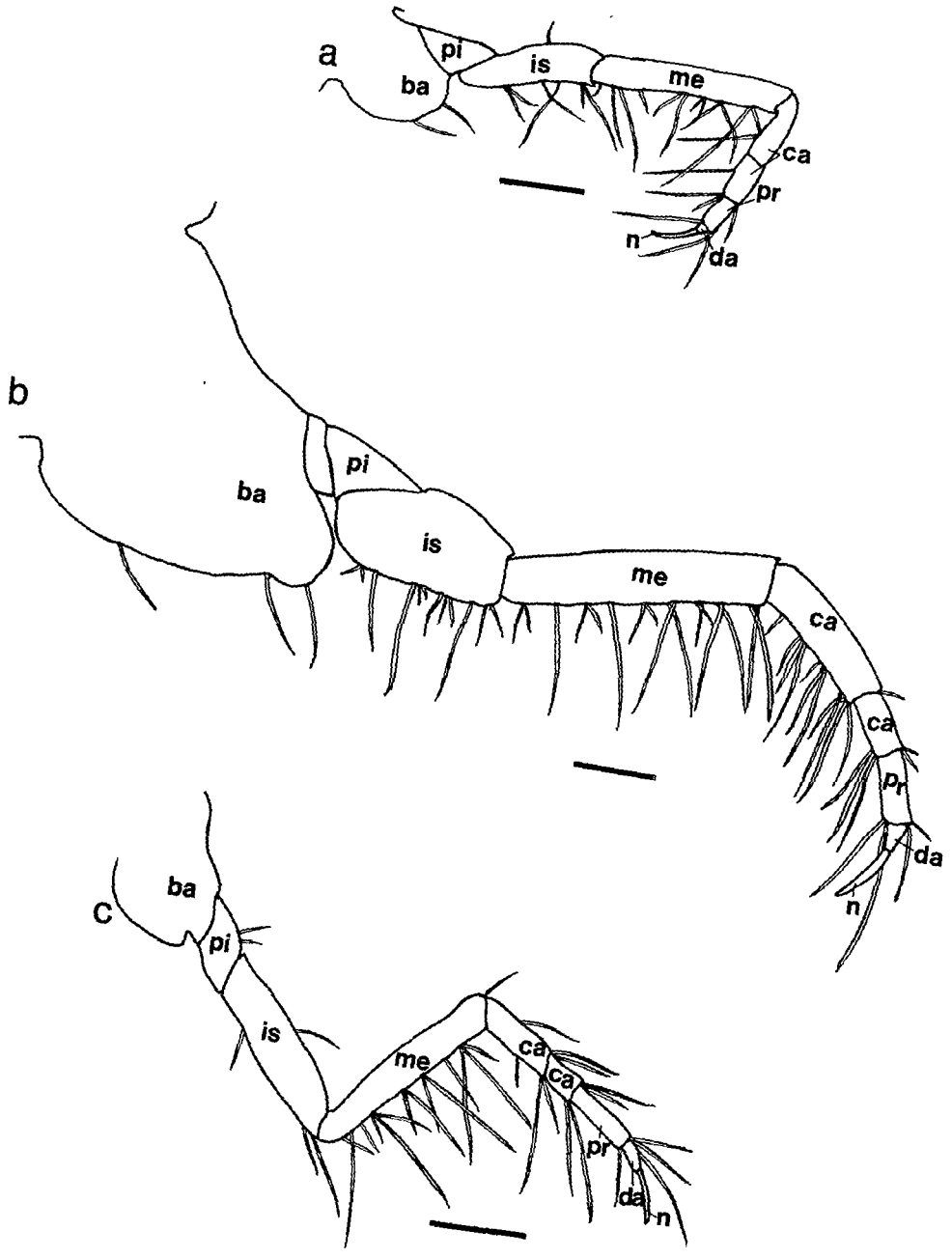

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Figure 8.2 The maxilliped II of the three mysid species. a. *Anisomysis mixta australis*: ba - basis, pi - pre-ischium, is - ischium, me - merus, ca-pr - carpo-propodus, da - dactylus, n - nail. b. *Paramesopodopsis rufa*: (abbreviations as in a). c. *Tenagomysis tasmaniae* (abbreviations as in a). Scale bars = 0.2 mm.

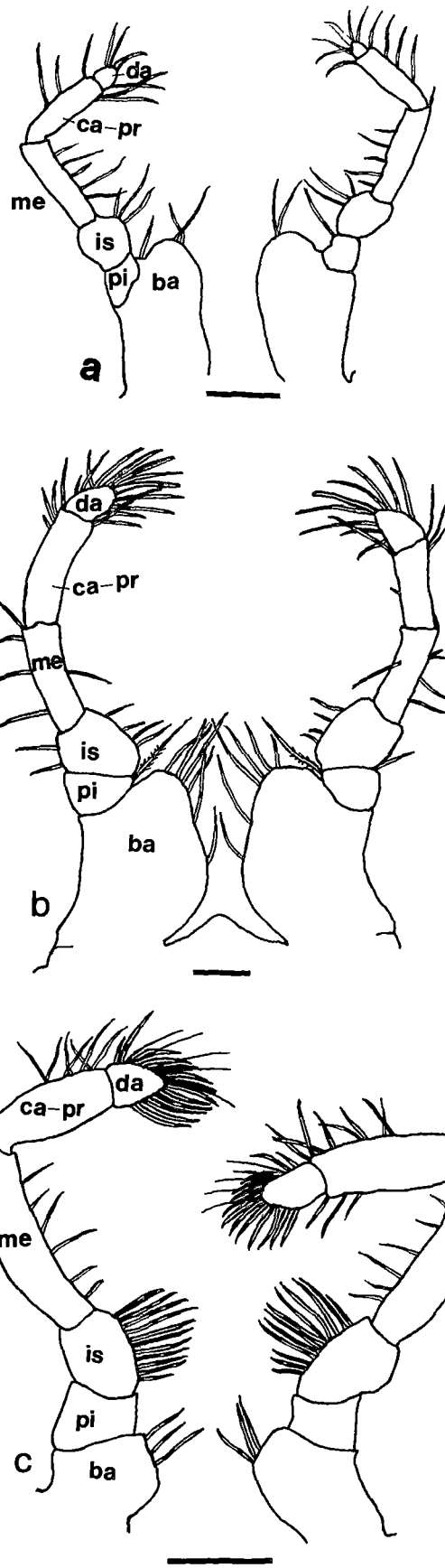
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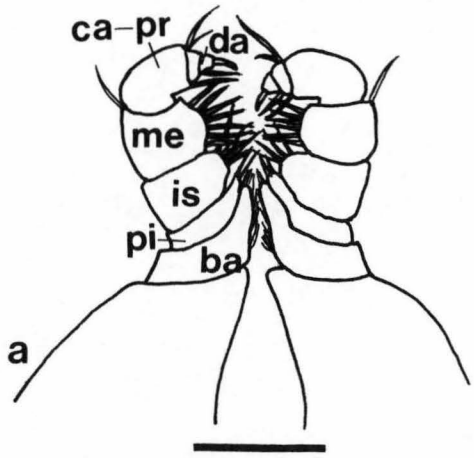
Figure 8.3 The maxilliped I of the three mysid species. a. *Anisomysis mixta australis*: ba - basis, pi - pre-ischium, is - ischium, me - merus, ca-pr - carpo-propodus, da - dactylus, n - nail. b. *Paramesopodopsis rufa*: (abbreviations as in a). b. *Tenagomysis tasmaniae* (abbreviations as in a). Scale bars = 0.2 mm.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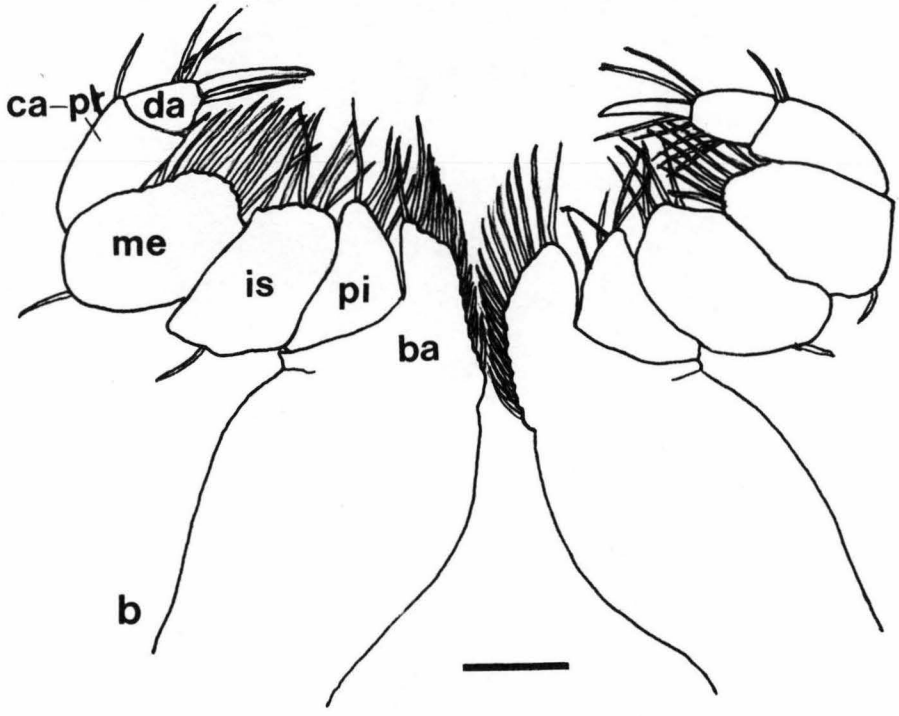
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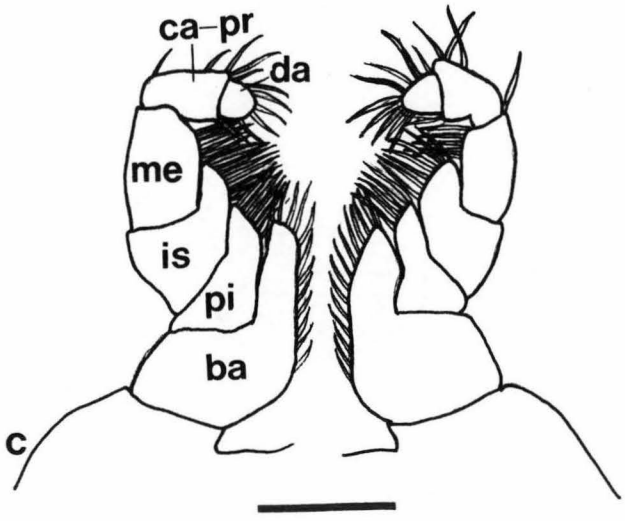
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Figure 8.4 The maxilla of the three mysid species. a. *Anisomysis mixta australis*: mp - maxillary palps, ex - exite, be - basal endite, 1 - proximal endite, 2 - distal endites. b. *Paramesopodopsis rufa*: (abbreviations as in a). c. *Tenagomysis tasmaniae* (abbreviations as in a). Scale bars = 0.2 mm.

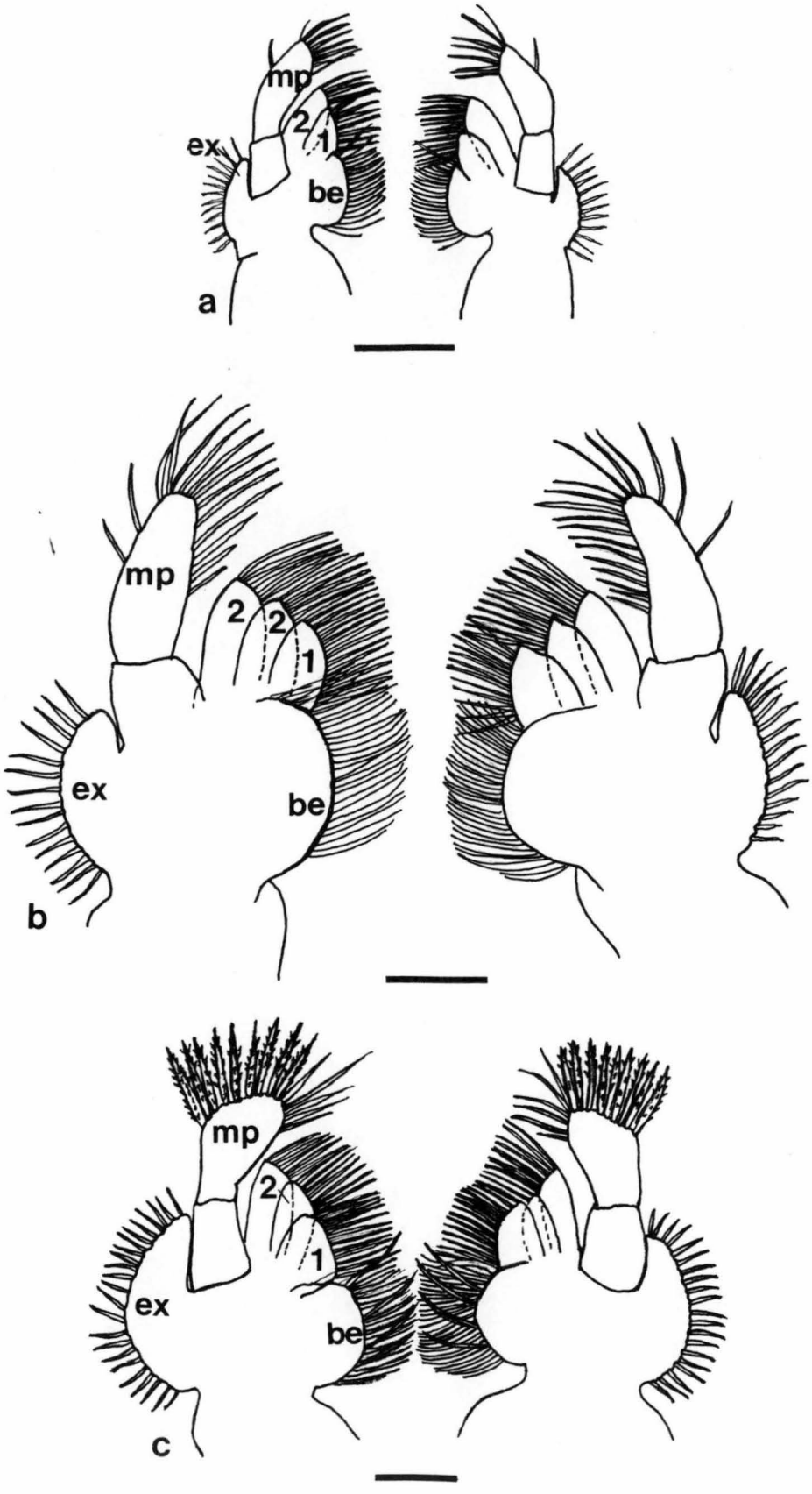
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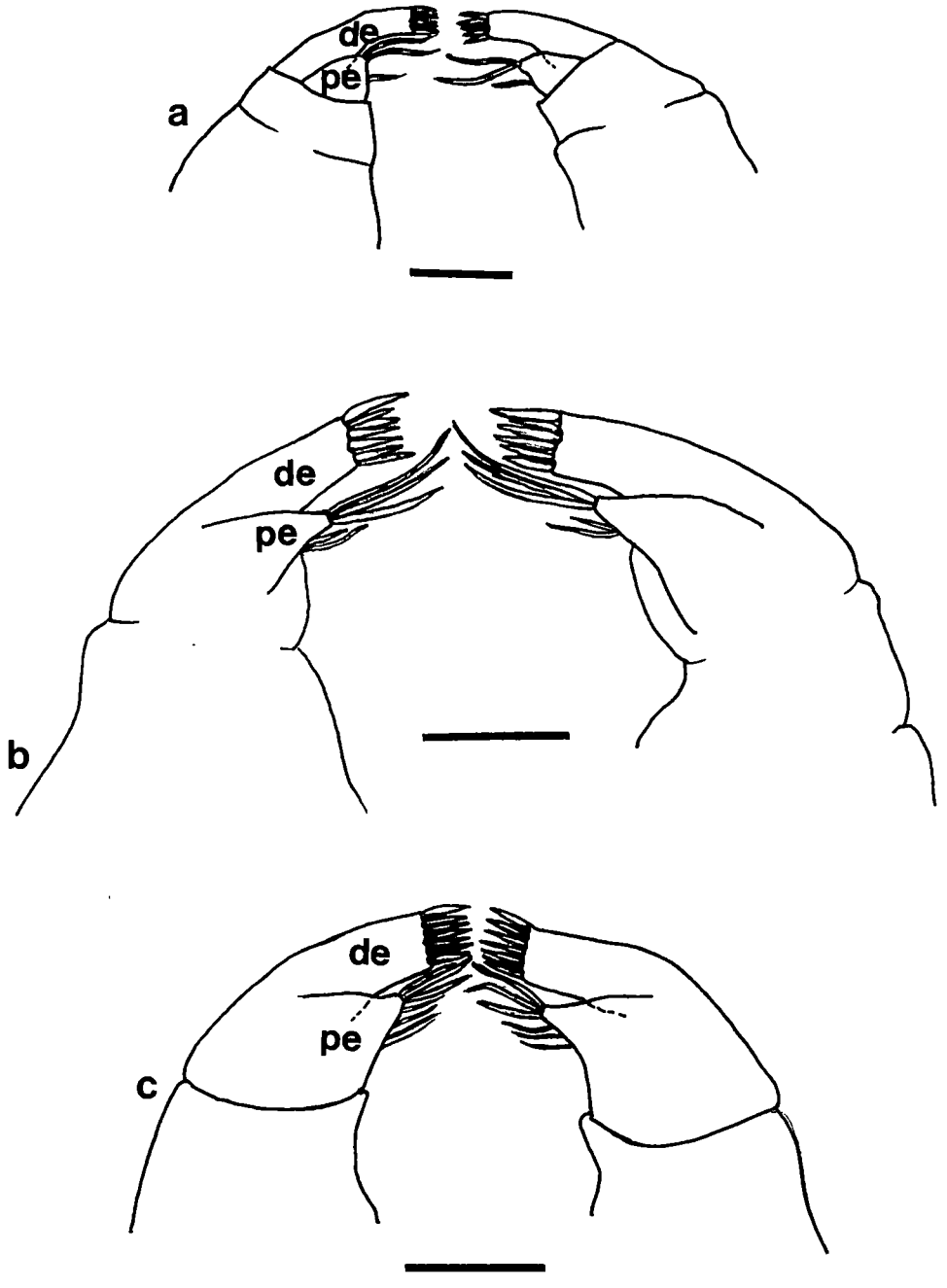
Figure 8.5 The maxillules of the three mysid species. a. *Anisomysis mixta australis*: pe - proximal endite, de - distal endite. b. *Paramesopodopsis rufa*: (abbreviations as in a). c. *Tenagomysis tasmaniae* (abbreviations as in a). Scale bars = 0.2 mm.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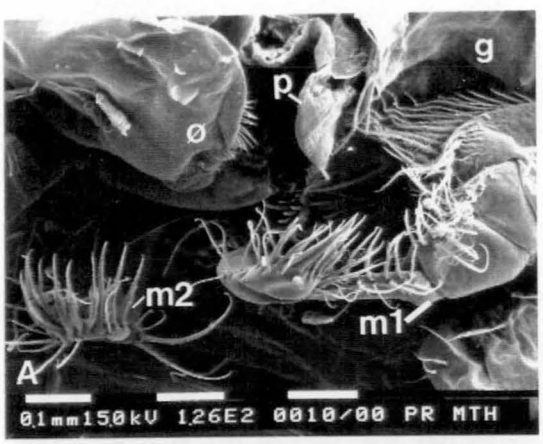
pe

Figure 8.6 SEM micrographs of *Paramesopodopsis rufa* mouthparts. A. Median lateral view of right side mouthparts: g - median groove of labium, m1 - maxilliped I, m2 - maxilliped II, p - labial paragnaths, ø - labrum. B. Median sagittal of anterior half of the animal showing cephalothoracic appendages: a - antenna, al - antennule, as - antennal scale, end - right endopods. C. Close -up of maxilliped II dactylus (d): + - stout sharp spines. D. Ventral view of maxillipeds I: d - dactylus, + stout sharp spine, s - plumose setae. E. Close-up of maxillary palp (mp): es - spines of the maxillular proximal endite. F. Close-up of labial paragnaths (p). G. Fine structure of setules on setae of maxillary proximal endite. H. Serrated setae on distal endites of maxilla. I. Left mandible armed edge: lm - *lacinia mobilis*, pi - *pars incisiva*, pm - *pars molaris*, sr - spine row. J. Close up of *lacinia mobilis* (lm) and spine row (sr). K. Close of *pars molaris*: D-region, ms - marginal spines, arrow points pore on the margin of grinding region. L. Fine structure of the grinding region teeth. M. Appendages of the left maxillule: de - distal endite, es - spines of the dorsal endite, pe - proximal endite. N. Close up of right mouthparts: es - spines of the maxillular distal endites, mb - right mandible, p - labial paragnaths, ø - labrum.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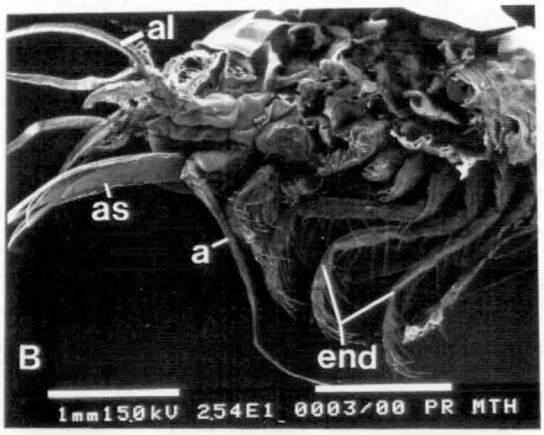
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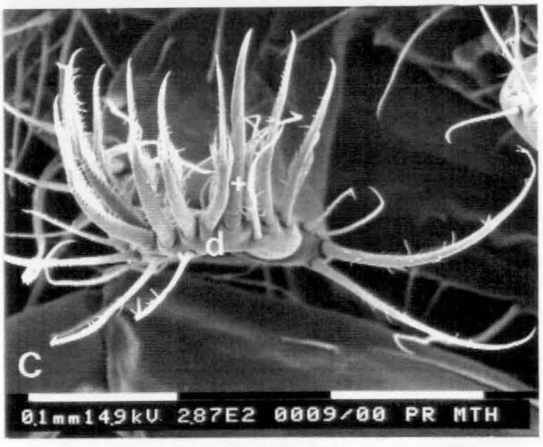
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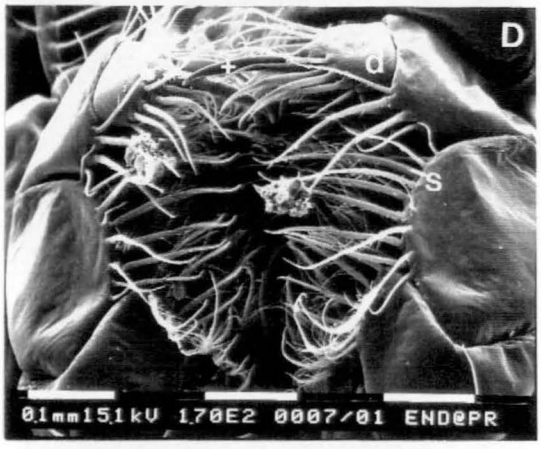
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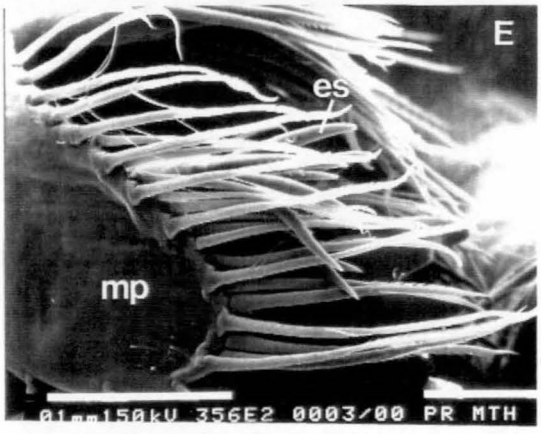
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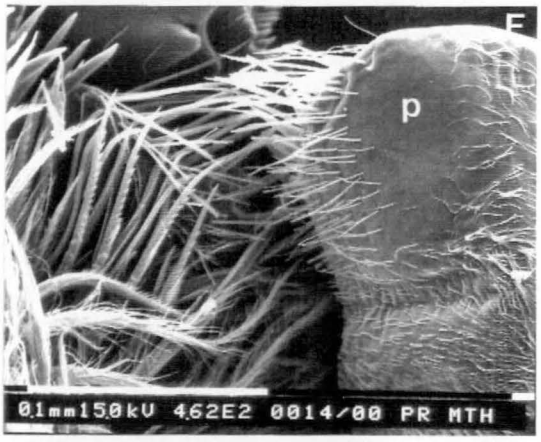
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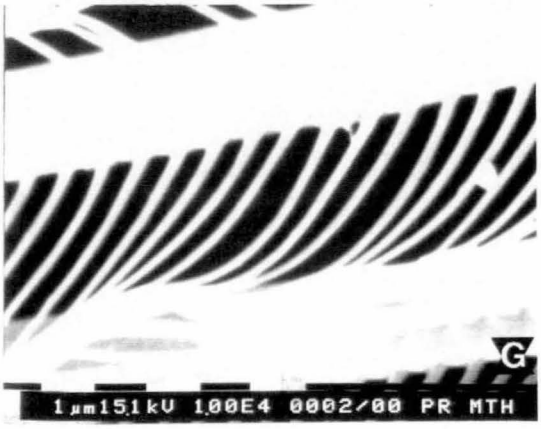
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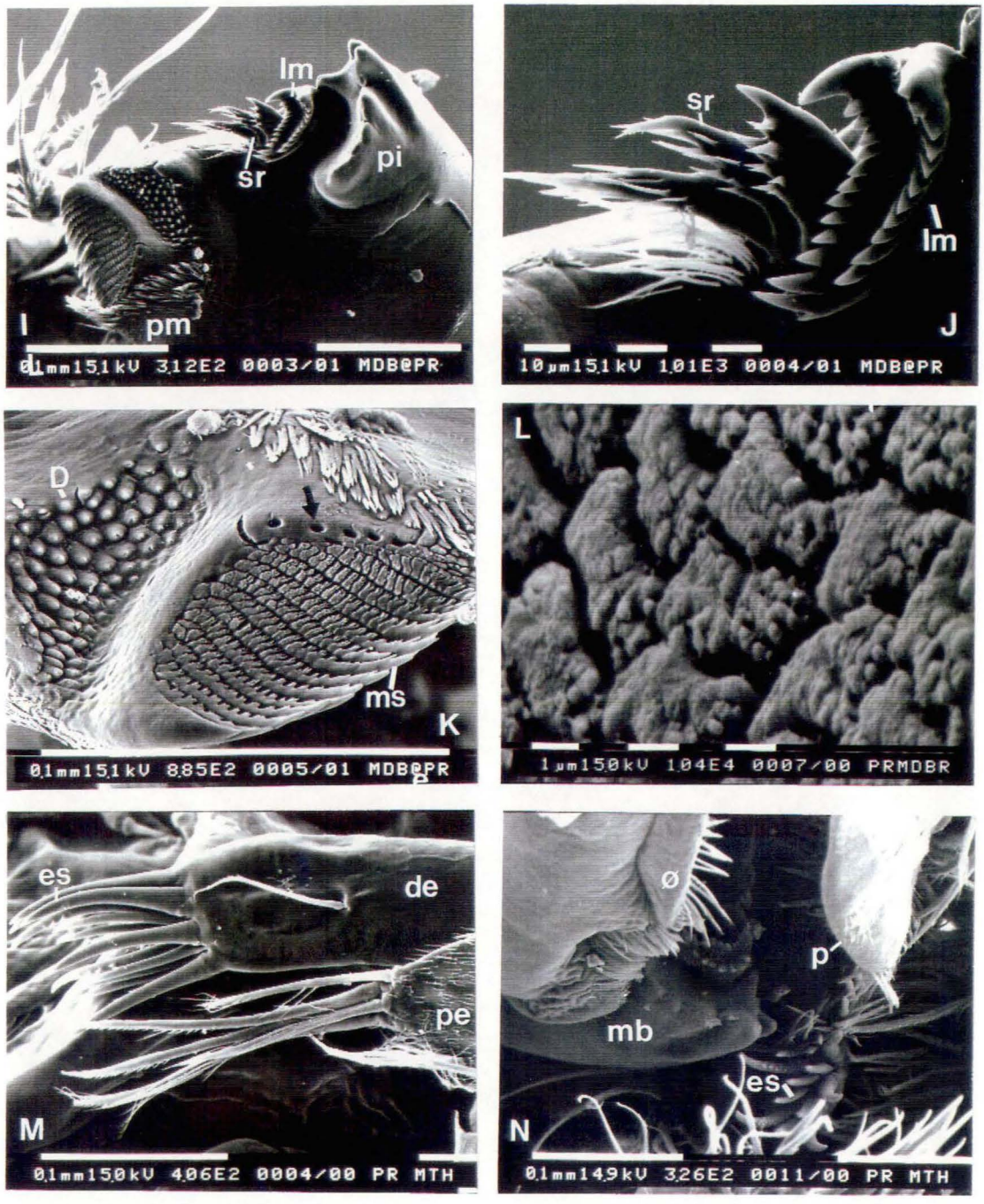
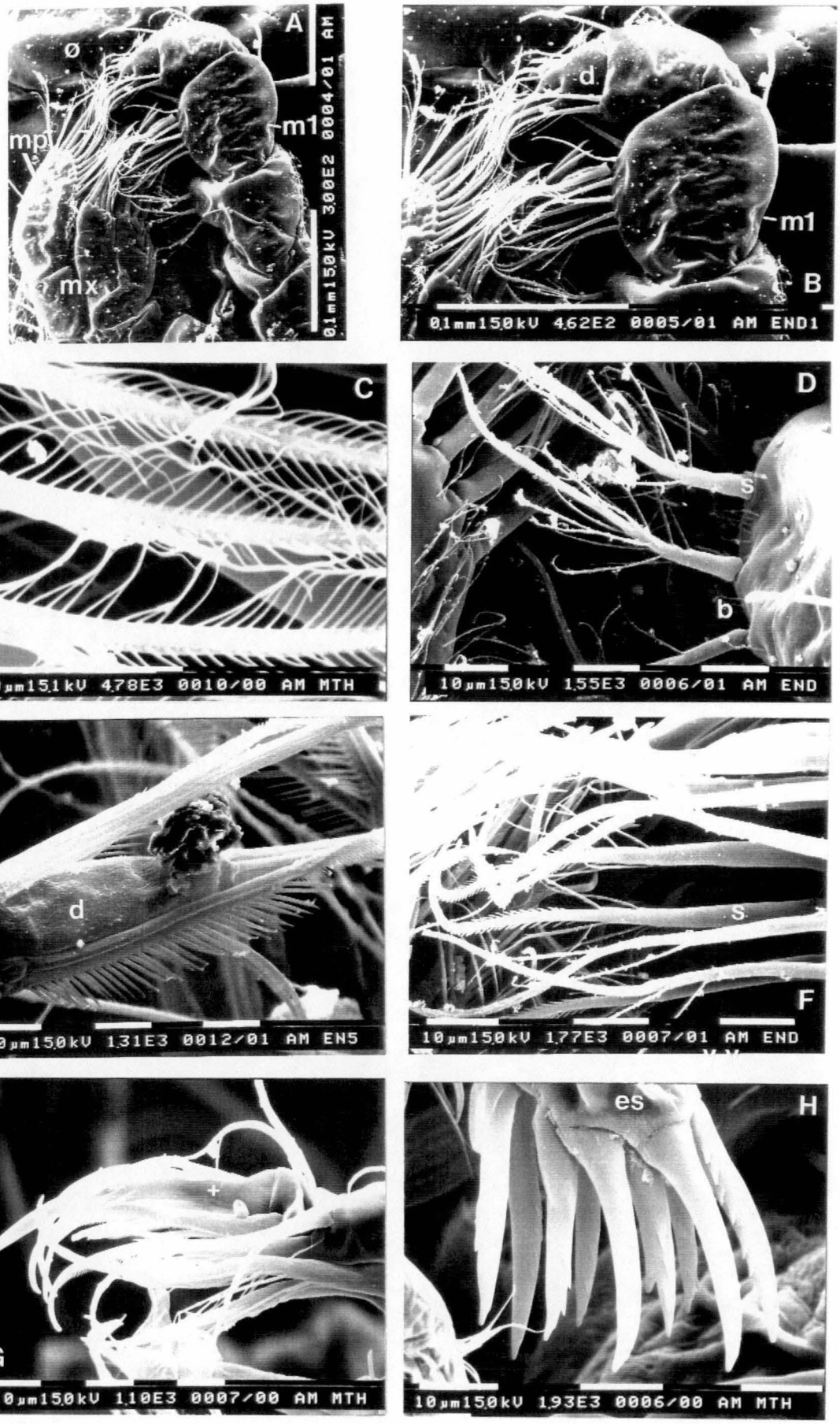


Figure 8.6 (continuation)

Figure 8.7 SEM micrographs of *Anisomysis mixta australis* mouthparts. A. ventral view of right maxilla (mx) and left maxilliped I (m1): ø - labrum. B. Close up of left maxilliped I: d - dactylus. C. Fine structure of setules on setae of maxillary exite. D. Setae (s) on the basal endite of left maxilliped I. E. Close up of the dactylus of thoracic endopod showing comb setae. F. Setae (s) on the merus of left maxilliped I. G. Dactylus of left maxilliped I: + - stout sharp spine. H. Close-up of the spines on the maxillular dorsal endite. I. Close up of left labial paragnaths (p): se - serrated setae of the maxillular proximal endite. J. Close up of cluster spines on the edge of labrum (ø). K. Posterior view of left mandible: lm - *lacinia mobilis*, pi - *pars incisiva*, pm - *pars molaris*. L. Fine structure of setules on setae of right maxilla proximal endite. M. Close-up of *pars molaris* (pm): ms - marginal spines, arrow points pore on the margin of grinding region. N. Fine structure of the *pars molaris* grinding surface: arrow as in M.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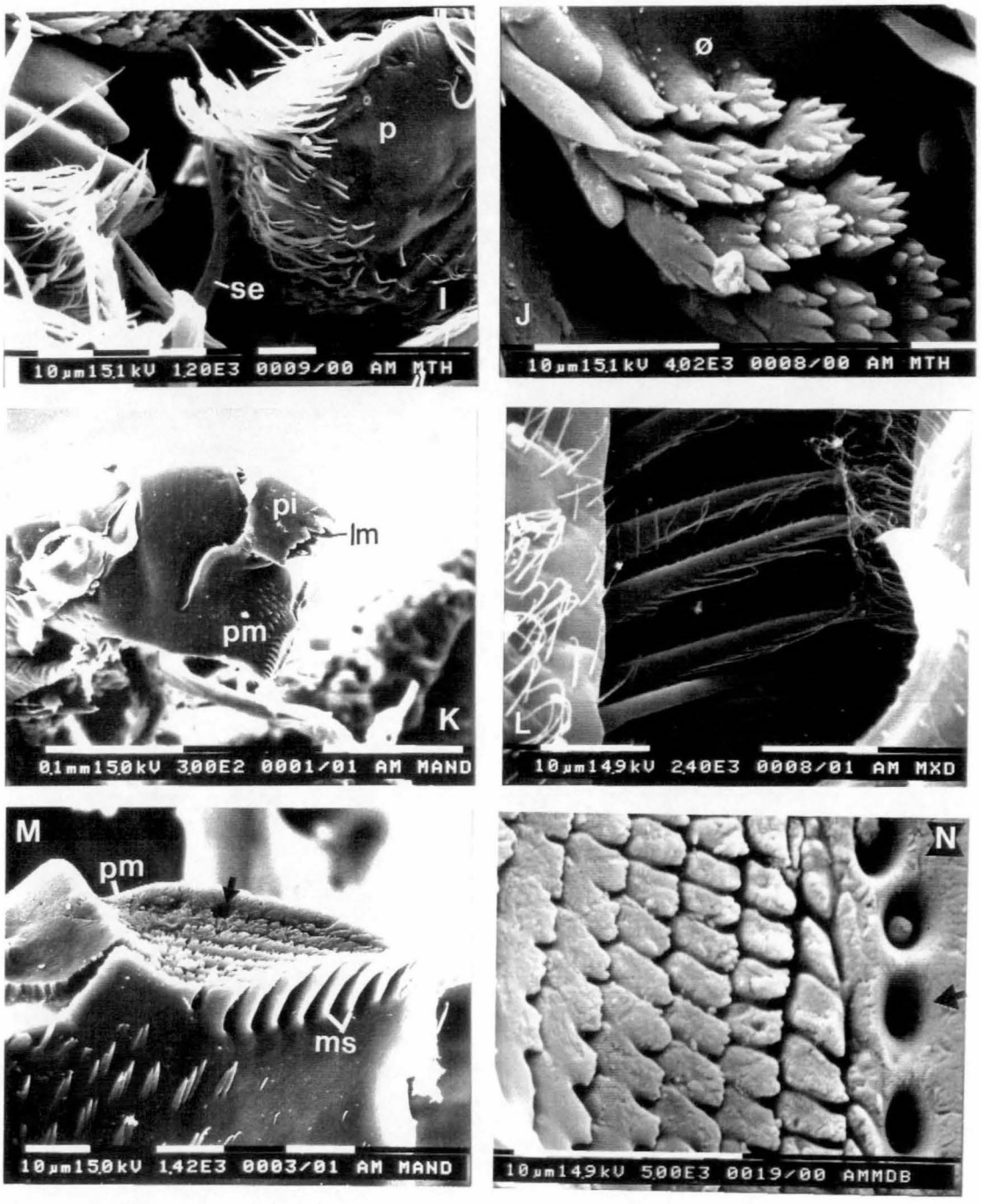
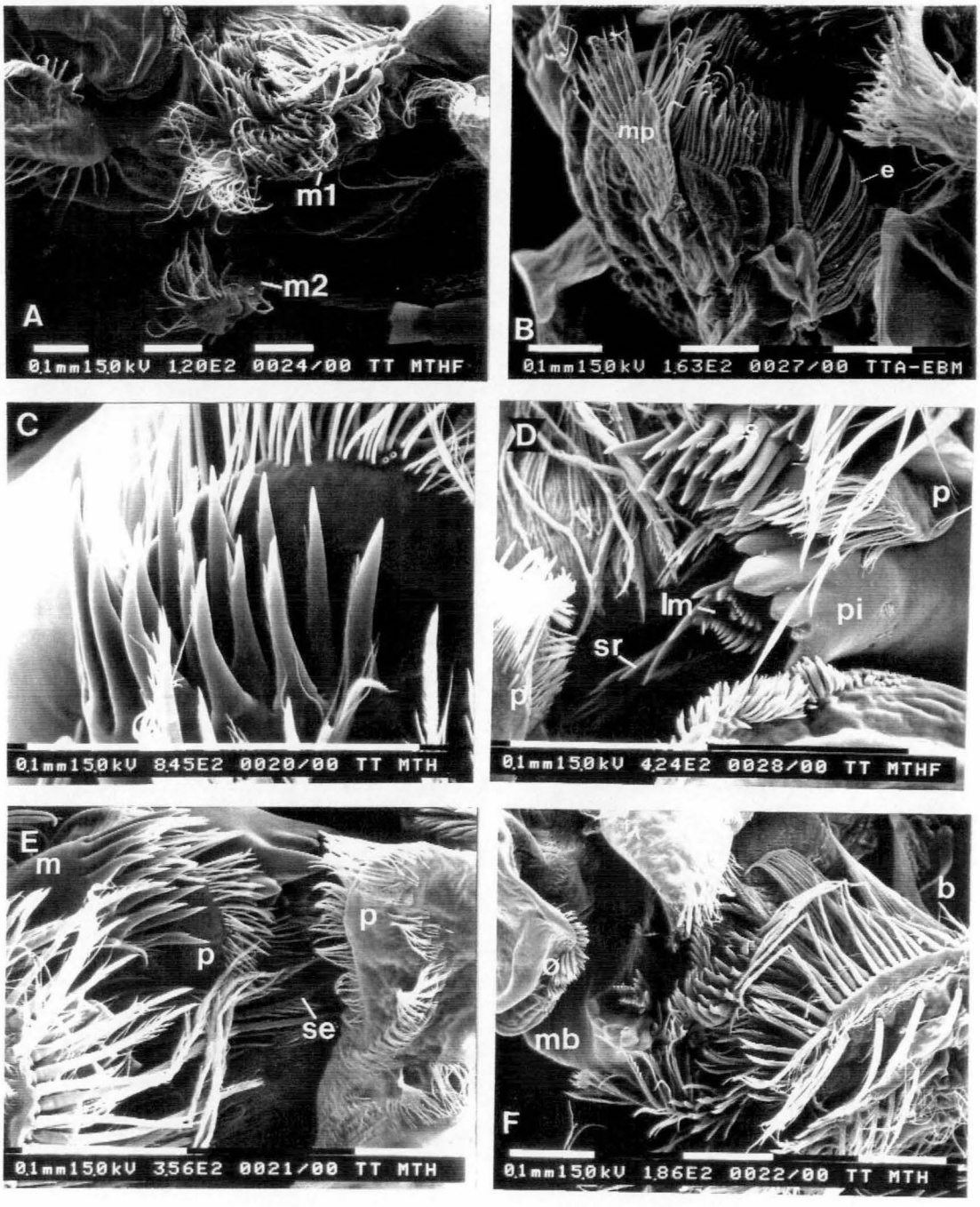


Figure 8.7 (continuation)

Figure 8.8 SEM micrographs of *Tenagomysis tasmaniae* mouthparts. A. Median lateral view of right side mouthparts: g - median groove of labium, m1 - maxilliped I, m2 - maxilliped II. B. Ventral view of maxillae: e - setae on proximal endite, mp - maxillary palp. C. Close-up of spines on the maxillular distal endite. D. Close up of ventral view of mouthparts: es - spines on the right maxillular distal endite, lm - *lacinia mobilis* of right mandible, p - labial paragnaths, pi - *pars incisiva* of right mandible, sr - spine row of right mandibel. E. Close-up of labial paragnaths (p): m - distal endite of right maxillule, se - serrated setae of the maxillular proximal endite. F. Median lateral view of right mouthparts: b - basal endite of maxilliped I, mb - right mandible, ø - labrum. G. Left mandible: lm - *lacinia mobilis*, pi - *pars incisiva*, pm - *pars molaris*, sr - spine row. H. Right mandible. I. Close up of *pars molaris* of left mandible: ms - marginal spines, arrow points pore on the margin of grinding region. J. Fine structue of *pars molaris* grinding region. K. Close-up of maxilliped II dactylus (d): s - serrated seta on apical edge of dactylus. L. Close-up of maxilliped I dactylus (d): s - as in K.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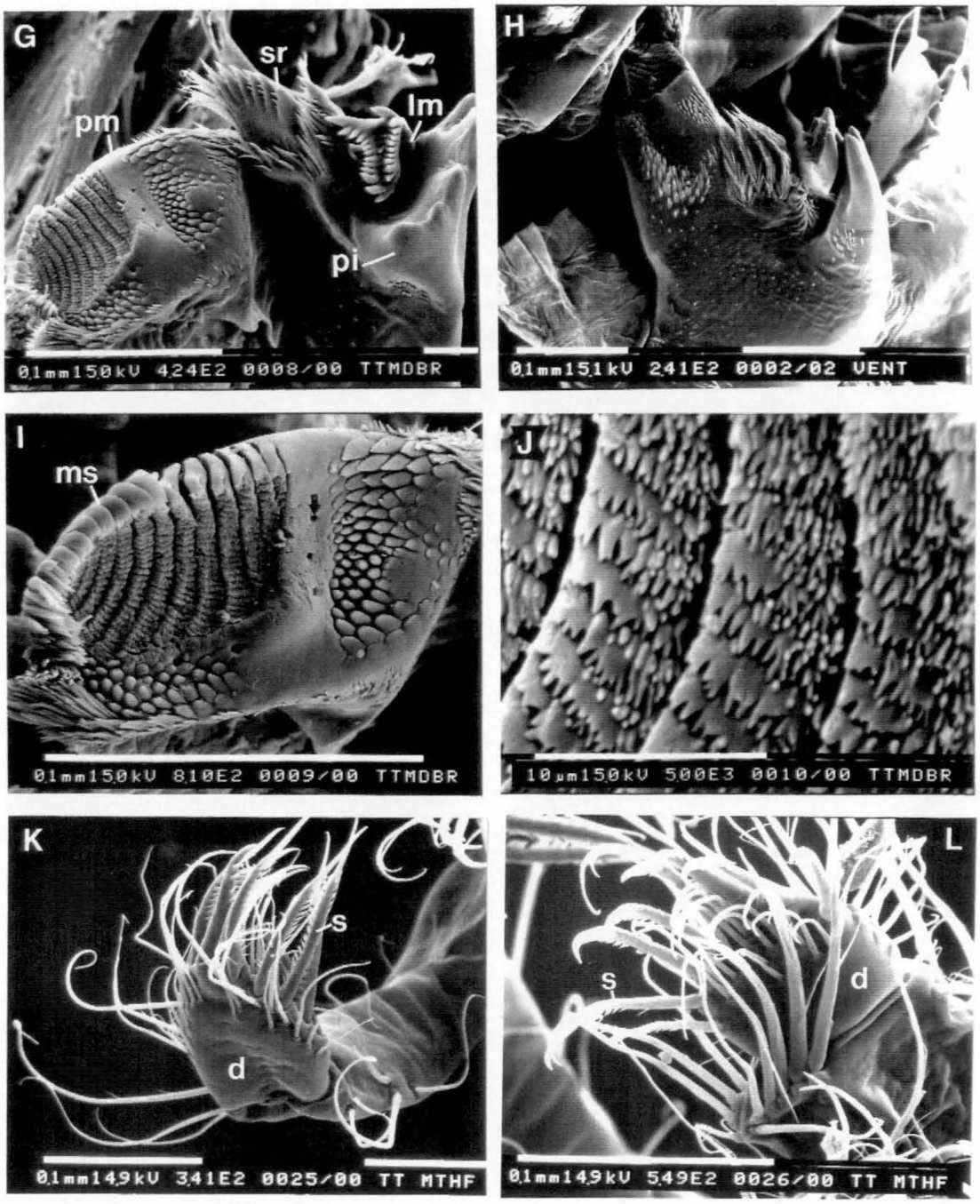

Figure 8.8 (continuation)

the thorax. The maxillary palps touch the ventro-posterior surface of the mandibular body. The setae arming the maxillary palp are different in the three species. Immediately lateral to the maxillary palp are three concave plates or endites, two distal and one proximal. The rows of serrated setae fringing the distal endites lie on the same plane as those of the maxillary palps while the setae on the proximal endite are curved towards the median food "groove" and lie on the same plane as those of the basal endite.

The maxillule is relatively simple, comprising ventral proximal and dorsal distal endites (Figs. 8.5, 8.6M) and is similar in the three species. The ventral endite bears bristled long setae which are in contact with the posterior face of the paragnath. The distal endite bears a bunch of slender and biting spines with a row of broad-based spinules on its inner shaft. These spines are ventral to the ventral edge of the paragnaths, and almost touch the base of the *pars incisiva* of the mandibles. Disposition and number of spines on the distal endite vary between the three mysid species.

No marked specialization is shown in the labia of the three species (Figs. 8.6F, 8.7I, 9.8E). The paired paragnaths of the labium border the posterior oral cavity with their concave anterior surfaces. The median edge of their anterior lobes are densely covered with thin, stiff, and bristled setae. These dense setae intermesh with each other forming a screen that fills up the space between the medial edges of both paragnaths. Small and fine setae are found on the ventral convex surface of the paragnaths. The labium becomes fused on its medial base forming a cleft or a median narrow groove.

The basic form of the mandibular palps is similar in the three species (Figs. 8.6I; 8.7K; 8.8G,H). All possess a pair of mandibles whose food-processing surfaces are asymmetric, dovetailing in the middle. The mandibular cutting edge of a typical mysid consists of four main elements which are all present on the left mandible. These edge structures are the *pars incisiva*, *lacinia mobilis*, spine row, and the *pars molaris*. The *lacinia mobilis* usually is reduced, if not lost among the edge

structures in the right mandible. The anterior aspect of the *pars molaris* wall bears patches of flat serrated spines occurring in groups of 3 or 4.

The labrum is thick and disc-shaped and forms the anterior border of the oral cavity (Figs. 8.6A,N; 8.7A; 8.8F). Flat, robust and setulose spines border the edge directly adjacent to the oral cavity. These features are shared by the three mysid species.

Differences in the Structure of Endopods and Mouthparts

Endopod Intersetal Gap

The intersetal spaces in the three mysid species ranged from 8 to > 118 μm, and their average relative frequency and the cumulative frequency are plotted in Figure 8.9. All three species showed a significant variation in their frequencies of intersetal distances (two factor analysis of variance: $F = 3.713$, df = 2, $p < 0.05$). Differences between species for a particular class intersetal distance were also highly significant (interaction: $F = 14.84$, df = 20, $p < 0.001$). It is interesting to note that average values of intersetal gaps in the three species intersect in the 52 to 62 μm intersetal gap class. Similar frequency values were shown by *Tenagomysis tasmaniae* and *Anisomysis mixta australis* for the lowest gap class, while *Paramesopodopsis rufa* had fewer values of this gap class. Highest frequency in *A. mixta australis* was in the 19 to 29 μm gap class. *T. tasmaniae* showed a peak at 41 to 51 μm. Peak in intersetal gap frequency in *P. rufa* occurred in the 74 to 84 μm gap class. In the same class, *T. tasmaniae* showed half the frequency, while very few of this size were recorded in *A. mixta australis*. No intersetal gaps > 96 μm occurred in *A. mixta australis*. *P. rufa* showed a higher frequency > 118 μm than in the other two species. The three species showed similar frequencies for the rest of the intersetal gap classes.

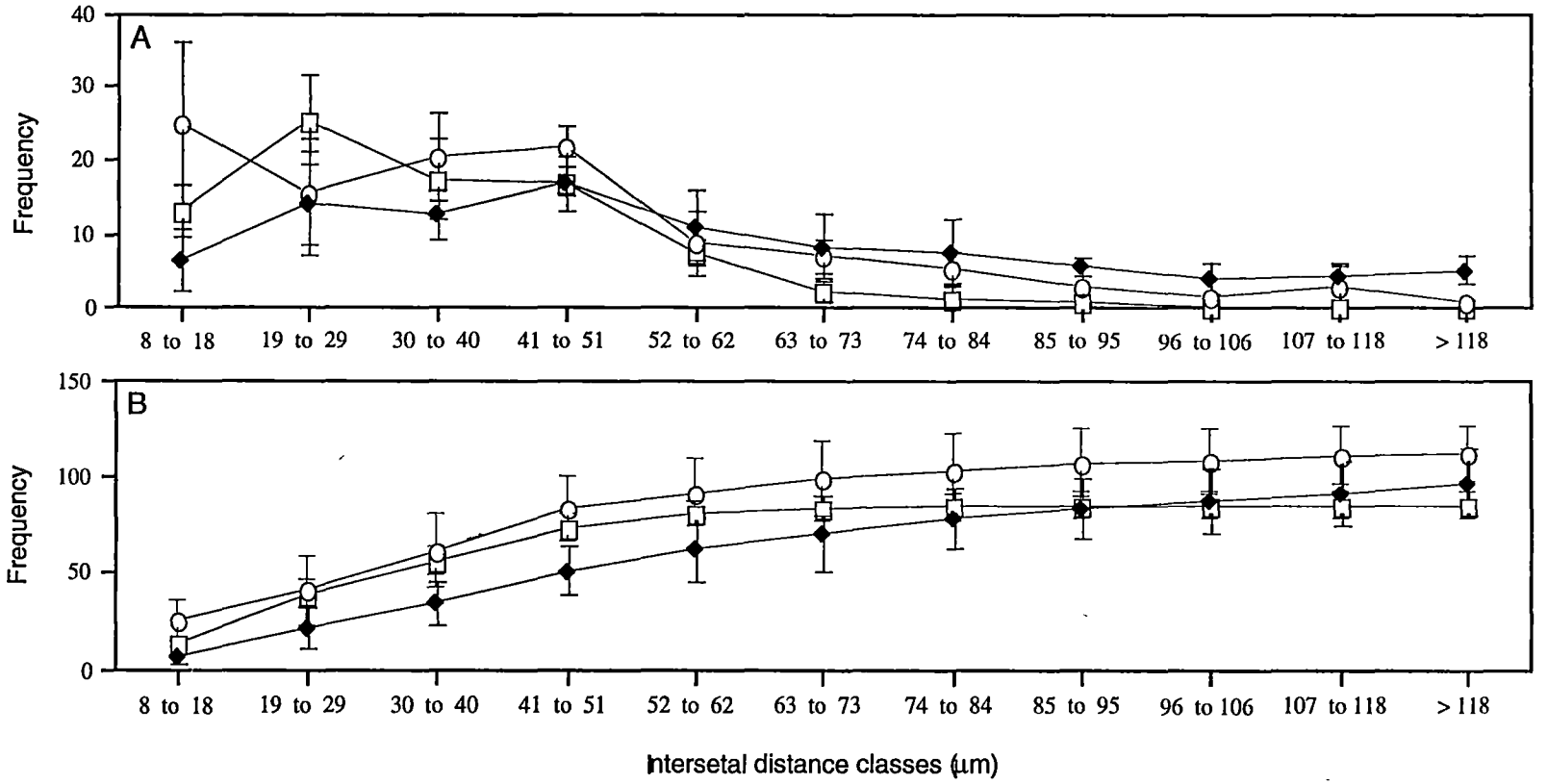

Figure 8.9 Mean intersetal distances on the thoracic endopods in the three mysid species. A. Frequency distribution. B. Cumulative frequency distribution. Squares - *Anisomysis mixta australis*, solid diamond - *Paramesopodopsis rufa*, circles - *Tenagomysis tasmaniae*.

Mouthparts

Paramesopodopsis rufa

Maxilliped II

The median edge of both the ischium and merus bears a row of widely spaced short setae. The transversely positioned carpus bears few long setae. The distal anterior edge of the propodus is lined by a row of long setae which form a rake-like structure with those lining the medial edge of the dactylus. Eight comb-like setae are present on the same edge of the dactylus, and parallel to these setae is the bristle-free stout spine very similar to that in the dactylus of maxilliped I (Fig. 8.6C).

Table 8.1 Intersetal and intersetular distances of the maxilla and maxilliped I in the three mysid species. (numbers in μm).

	Paramesopodopsis rufa	*Anisomysis mixta australis*	*Tenagomysis tasmaniae*
Maxilla			
Endite intersetal gap (range)	3.4 - 6.2	3.9 - 4.94	6.9 - 9.0
Endite setae intersetular gap (range)	0.35 - 0.74	0.5 - 0.8	0.38 - 0.55
Maxilliped I			
Endite intersetal gap (range)	8.1 - 13.3	4.3 - 10.4	3.2 - 6.9
Endite setae intersetular gap (range)	5.0 - 11.6	2.5 - 6.9	9.0 - 14.8

Maxilliped I

The basis bears a plate-like endite, the edge of which is fringed with a row of long and plumose setae (Fig. 8.6A,D). The tips of these setae touch portions of the median groove of the labium. The tips of the longer setae touch the posterior surface

of the labial paragnaths. The anterior edge of the ischium is fringed with stout and setulose setae. The merus, like the ischium bears similar types of setae on its anterior edge. Lying horizontally and pointing anteriorly is the carpus which bears rows of stout bristled setae on its medial surface. The propodus curves medially and bears a few bristled setae which form a mesh with those on the carpus. Pointing medially, the dactylus has thin and stout setae on the edge of its tip (Fig. 8.6D). These setae are coplanar with those found on the ischium, merus, carpus and propodus and form a "screen". Intersetal gaps of these podomeres ranged from 8.1-13.3 μm and intersetular gaps of these setae ranged from 5.0-11.6 μm (Table 8.1). The dactylus of maxilliped I bears a stout and sharp spine.

Maxilla

The maxillary palp of this species is fringed with comb setae which are of a similar type to those in *A. mixta australis* (Fig. 8.6E). However, these setae appear more dense in *P. rufa* than in *A. mixta australis*. Gaps between these setae ranged from 3.4-6.2 μm. The setae fringing the basal endite have setules forming a mesh (Fig. 8.6G). In *P. rufa*, the intersetular distance of the mesh ranged from 0.35-0.74 μm (Table 8.1).

Table 8.2 Edge Index and other features of the right mandibles of the three mysid species. (numbers in μm).

	Paramesopodopsis rufa	*Anisomysis mixta australis*	*Tenagomysis tasmaniae*
Edge Index (*pars molaris*/ *pars incisiva*)	1.14 ± 0.06	1.24 ± 0.00	1.63 ± 0.20
pars incisiva teeth gap (range)	5.7 - 31.7	2.2 - 9.3	7.7 - 20.9
pars molaris teeth groove gap (range)	3.9 - 6.4	1.3 - 2.4	3.5 - 4.8
pars molaris number of teeth rows	8	12	13

Maxillule

The distal endite of the maxillules possess 12 spines which have blunt tips and few broad based spinules (Fig. 8.6M,N).

Mandible

The 1.14 ± 0.06 mandibular edge index for *P. rufa* is the smallest of all three species (Table 8.2). The left mandible of *P. rufa* bears the *pars incisiva* with seven blunt peaks (Fig. 8.6I) 5.7-31.7 μm apart (Table 8.2). Bearing two rows of stout sharp spines, the *lacinia mobilis* is dorsal to the *pars incisiva* and its ventral convex surface fits the concavity of the *pars incisiva* (Fig. 8.6I,J). Fourteen spines arm the dorsal row while the ventral row has 11. The largest spine on each row is the most anterior. These spines become shorter towards the middle spine, while the lengths increase towards the posterior end. The mandibular spine row is composed of three powerful stout spines each of which bears on its posterior aspect very sharp, broad and thin-based spinules (Fig. 8.6I,J). The three spines are fused at their bases. A patch of setae is found adjacent to the third spine of the spine row. The region between the spine row and the base of the *pars molaris* is devoid of any cuticular projections.

The gross shape of the *pars molaris* is cylindrical with its elevated heavily armed surface at the level of the *pars incisiva* (Fig. 8.6I,K). The *pars molaris* consists of a "squeezing" or "crushing" D-region where round based and blunt projections are found, and a grinding region composed of 12 rows of teeth with groove gaps ranging from 3.9-6.4 μm (Table 8.2). The dorsal margins of these rows of teeth are knife-like (Fig. 8.6K). Five to six large pores are present on the anterior margin of the grinding region (Fig. 8.6K). The dorsal corner of the grinding region has a tuft of flat spines, and long stiff setae. The teeth in the grinding region are blunt (Fig. 8.6L).

Anisomysis mixta australis

Maxilliped II

The fewer setae on the second maxillipeds distinguishes *A. m. australis* from the other two species (Fig. 8.2A). A few of the serrated setae are found on the dactylus, and as in *P. rufa*, a stout spine is present on this podomere.

Maxilliped I

The distinctive feature of the maxillipeds I in *A. m. australis* is the reduced number of setae on the different podomeres (Fig. 8.7A,B). Few serrulate setae are found on the merus. Only two plumose setae which lie on the same plane as the meral setae are found on the carpus (Fig. 8.7F). Few setae are also found on the fused carpo-propodus. Gaps between these setae ranged from 4.3-10.4 µm (Table 8.1). A terminal stout spine is present on the dactylus of maxilliped I (Fig. 8.7G). The basal endite of this mouthpart only bears three of the plumose type of setae (Fig. 8.7D) with widely spaced setules ranging from 2.5-6.9 µm.

Maxilla

The proximal endite bears finely setulated setae (Fig. 8.7C) and the inter-setular distances range from 0.5-0.8 µm (Table 8.1). The two plates of the distal endites bear plain plumose setae, and few of the sharply serrated setae (Fig. 8.7A). The most distal portion of the maxillary palp is fringed with few simple plumose setae which, like those in the distal endite plates, form a single row (Fig. 8.7A). Intersetal gaps of the endites ranged from 3.9-4.9 µm (Table 8.1).

Maxillule

The distal endites of the paired maxillules bear 9 sharp spines with few broad based spinules (Fig. 8.7H).

Mandible

The cutting edges of the *pars incisiva* are at the same level as those on the *pars molaris* (Fig. 8.7K). Six triangular teeth (gap range = 2.2-9.3 µm (Table 8.2)) are present in the *pars incisiva* while four teeth are present in the *lacinia mobilis*. The three barbed spines which comprise the spine row are fused at their bases. A small patch of flat spines arises from the base of the *pars incisiva*. The right mandible has

no spine row, and its *pars molaris* bears no "squeezing" or D region. However, the *pars molaris* of the left mandible has seven rows of teeth which terminate as sharp marginal spines (Fig. 8.7M). A bunch of long and stiff setae are present on the dorsal part of the *pars molaris*., and like in *P. rufa*, this structure consists of the "squeezing or crushing" D-shaped region on which dome-shaped thickenings are found, and the grinding region with rows of teeth. The gaps between these rows ranged from 1.3-2.4 μm (Table 8.2). A row of pores lies on the posterior margin of the grinding region; four of these are large and one small (Fig. 8.7N). The small pore lies closer to the D region of the *pars molaris*. The mandibular edge index for *A. mixta australis* is 1.24 which is between those of the other two species (Table 8.2).

Tenagomysis tasmaniae

Maxilliped II

The maxillipeds II in *T. tasmaniae* differ from those in the other two species by the presence of closely spaced setae on their ischia (Fig. 8.2C). The other segments contain few setae except the dactylus which ventrally has long and slender setae. The edge of the dactylus bears 7 setae which are robust, serrated, and with pointed and curved tips (Fig. 8.8K). The dactylus of the maxilliped II lacks the sharp spine characteristic of those in the other two species.

Maxilliped I

The basal endite comprises two sets of setulated setae arranged in a single row (Fig. 8.8F). Six of these long and finely setulated setae are found on the most distal portion of the endite interspersed with fifteen other long but strongly serrated stout setae. These setae are in contact with the row of setae on the basal endite of the maxilla. The tips of the long setae extend up to the base of the medial cleft of the paragnaths (Fig. 8.8E). Measurements of intersetal gaps ranged from 3.2-6.9 μm and intersetular gaps 9.0-14.8 μm (Table 8.1). With the exception of the dactylus, the remaining segments of maxilliped I bear rows of long plumose setae. The dactylus lacks the spine present in the other two species. Short and thin setae form a patch on

the dorsal aspect of this segment. Interspersed among these setae are 7 stout and strongly serrated setae with curved tips (Fig. 8.8L).

Maxilla

In *T. tasmaniae*, each of the 13 to 14 double serrated setae on the apical edge of the maxillary palp is characterized by sharper and stouter setules projecting from the distal half of the shaft (Fig. 8.8E). Intersetal distances ranged from 6.9-9.0 μm while the intersetular distance from the setae of the basal endite ranged from 0.38-0.55 μm (Table 8.1).

Maxillules

The spinous distal endite of the maxillules in *T. tasmaniae* is wider and bears 14 biting spines sharper than those in the other two species (Fig. 8.8C,D,E).

Mandible

T. tasmaniae showed the highest (1.63 ± 0.20) mandibular edge index indicating a much larger *pars molaris* compared to those in the other two species (Table 8.2). The *pars incisiva* possesses five cutting teeth (Fig. 8.8G) 7.7-20.9 μm apart (Table 8.2). The form of the *lacinia mobilis* is similar to that in *P. rufa* (Fig. 8.8G). However, fewer spines are present on its ventral row (10) and on the dorsal row (12). Projecting perpendicular to the *lacinia mobilis* is the spine row which is flanked on its ventral and dorsal side by a bunch of flat, long and stiff setae. The spine row consists of six blade-like spines with 3-4 anterior broad-based spinules (Fig. 8.8G). These spines share a common base on which flat and long spines originate. The area between the spine row and the *pars molaris* bears a dense projection of these spines.

The *pars molaris* region includes a grinding surface which comprises 13 slightly overlapping rows of wider and larger teeth (Fig. 8.8I; Table 8.2) with very sharp cusps (Fig. 8.8J). The gap between these rows of teeth ranged from 3.5-4.8 μm (Table 8.2). On the margins where each row terminates, the teeth become stout spines which are curved towards the surface of the grinding region. The dorsal marginal teeth become a bunch of sharp and flat spines. Adjacent to these structures is a tuft of long flat setae. The ventral ridge of the grinding region reveals a row of

three small pores, while the anterior ridge bears two large pores (Fig. 8.8I). The ventral ridge separates the grinding region from the "squeezing and shearing" region. The shearing region is armed with large, flat, and sharp spines as well as round-based and blunt tipped spines.

All the different structures of the left mandible except the spine row are present in the right mandible (Fig. 8.8H). The *lacinia mobilis* possesses three blunt teeth which are slightly above the teeth of the *pars incisiva*. The spine row of the right mandible is composed of four rows of long and short soft setae which are curved towards the ventral aspect of the *pars molaris*. A patch of dome-shaped spines is found below the anterior ridge of the grinding region. Pores are also present on the ridges bordering the grinding region. The marginal teeth of each row are not curved and spine-like, but are similar in dentition to the rest of the teeth. The most dorsal margin of the grinding region also bears a tuft of flat, long and stiff setae.

The Structure of the Foregut

Gross Morphology of the Mysid Foregut

The general foregut structure is similar in the three species of mysids (Fig. 8.10), thus transverse sections are only shown for one species (Fig. 8.10B.1 to B.6). Foregut features in common are described here briefly. Storch (1989) provides detailed coverage. For convenience in the description and homology of structures, the terminology used by Storch (1989) is followed.

The chitinous foregut is divided into anterior cardiac, middle pyloric, and posterior funnel regions. At the junction between the oesophagus and the anterior cardiac region, a cardio-oesophageal valve projects anterodorsally. Behind the valve is the spine-bearing pre-anteromedianum ridge, the lateral margins of which meet the ventral margins of the anterior lateralia. The roof of the cardiac chamber is devoid of any projections, except the prominent dorsal fold. Cuticular ridges armed with spines are situated on the lateral and ventral regions (*e.g.* Figs. 8.10, 8.11A, 8.12A, 8.13A, 8.14A). The bilaterally symmetrical lateralia form the most conspicuous cuticular

Figure 8.10 Diagrammatic internal lateral view of right side of the foregut of three mysid species (inferomedianum not in longitudinal section to show the secondary filters). A. The foregut of *Paramesopodopsis rufa*. B. The foregut of *Anisomysis mixta australis* with transverse sections (B.1-B.6) of the different regions; arrows indicate the sectioned region. C. The foregut of *Tenagomysis tasmaniae*. Abbreviations: als - anterolateral spines; am - anteromedianum; as - spines on anterior laterale; cc - cardiac chamber; cdfc - cardiac dorsal food channel; cdlt - cardiac dorsolateral tooth; cdp - cardiac dorsal piece; cov - cardio-oesophageal valve; cr - cardiac region; cvfc - cardiac ventral pyloric channel; cvlt - cardiac ventrolateral tooth; df - dorsal fold; dlcc - dorsolateral circulation channel; f - funnel; fr - funnel region; g - groove of secondary filtration channel; il - inferolaterale; im - inferomedianum; l - laterale; lcc - lateral circulation channel; oe - oesophagus; pamr - pre-anteromedianum ridge; pdfc - pyloric dorsal food channel; pf - primary filter; pls - posterolateral spines; pr - pyloric region; psl - pyloric superolaterale; s - spigot.

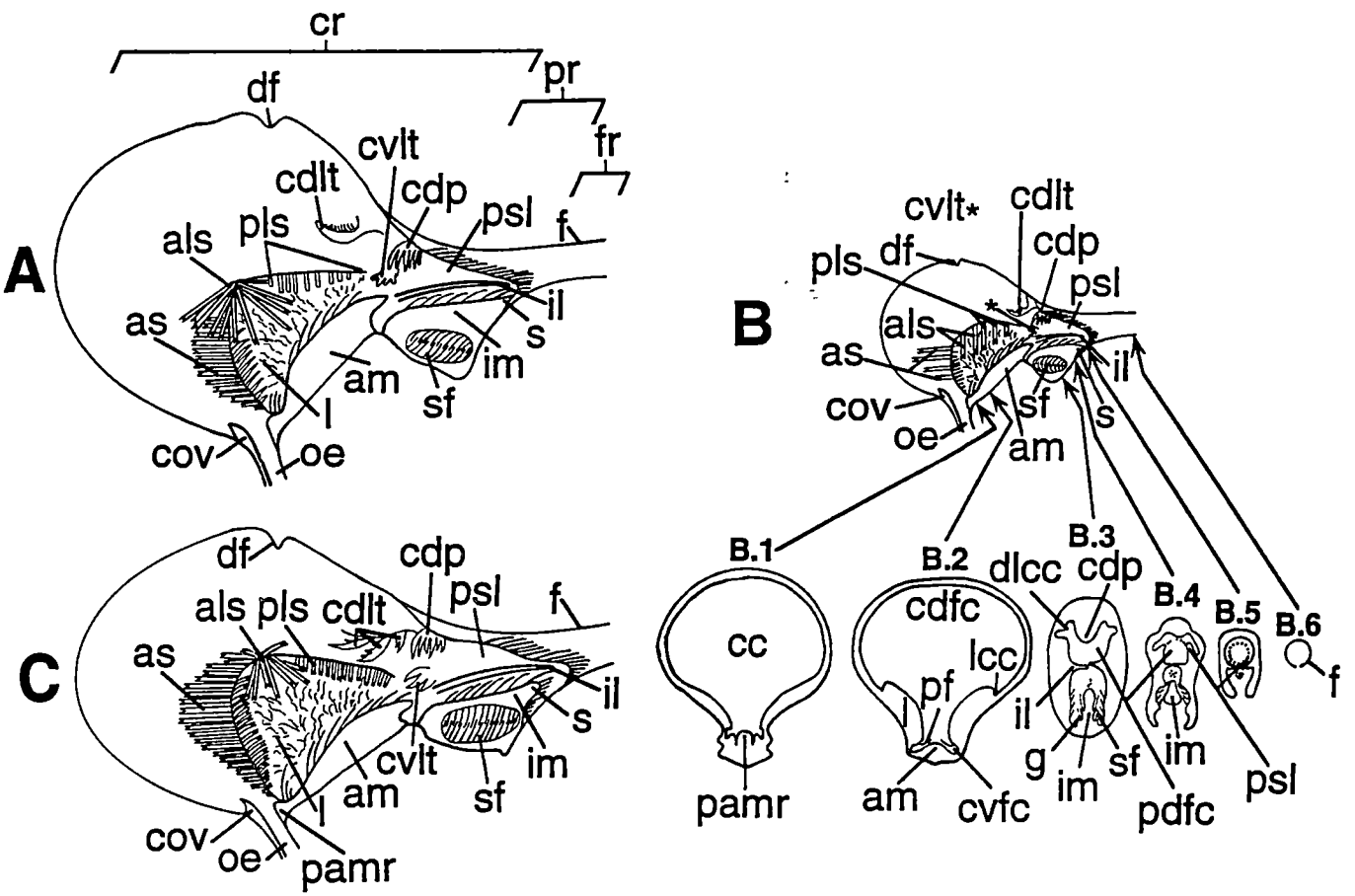
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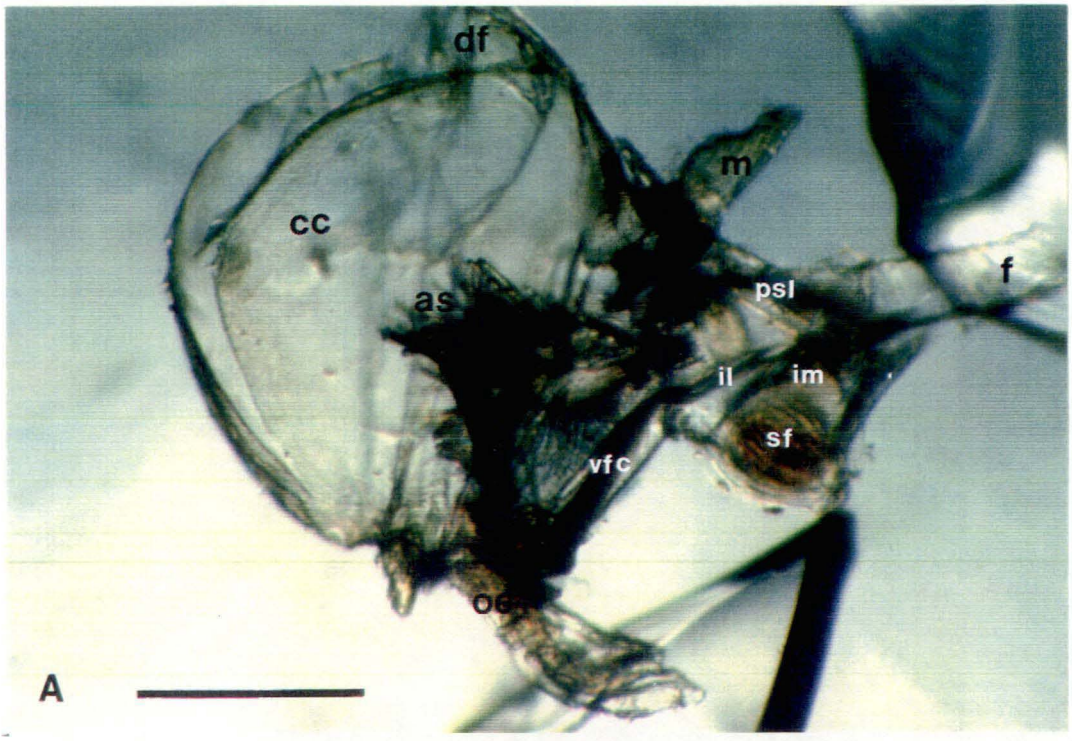
Figure 8.11 Light micrographs of *Paramesopodopsis rufa* foregut. A. Lateral view showing the spacious anterodorsal cardiac chamber (cc), dorsal fold (df), dorsal muscle (m), oesophagus (oe), the spines of the anterior laterale (as), ventral filtration channel (vfc), posterior superolaterale (psl), secondary (gland filter) (sf), and funnel. B. Anterodorsal view showing als, am, as, cc, cdlt, cdp, pamr, pls. C. Dorsal view, showing als, as, cc, and psl. Scale bar: A-C = 170.3 μm.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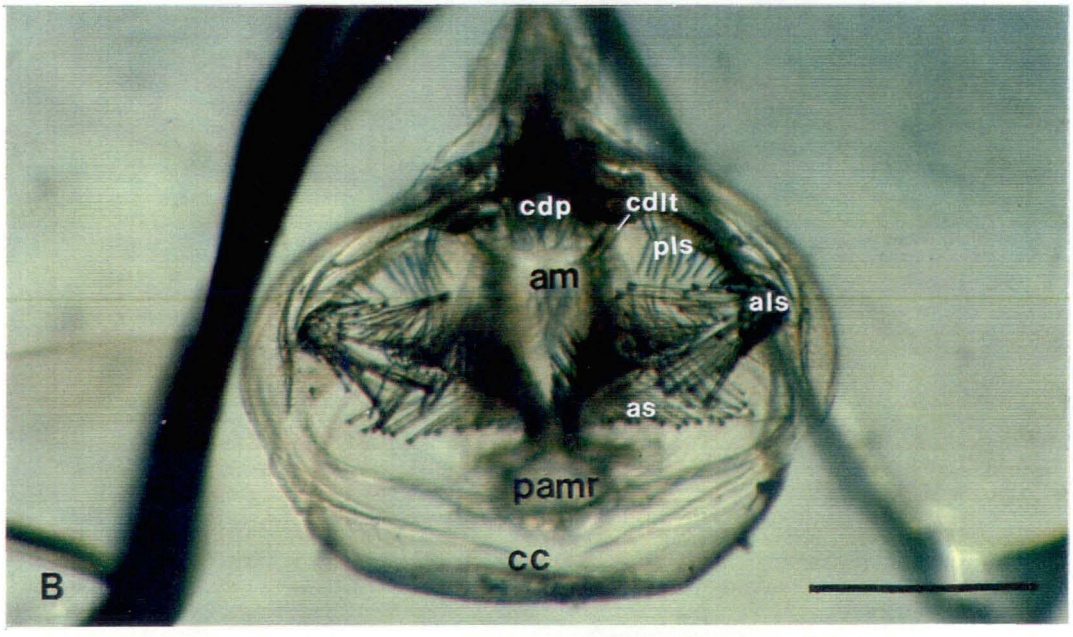
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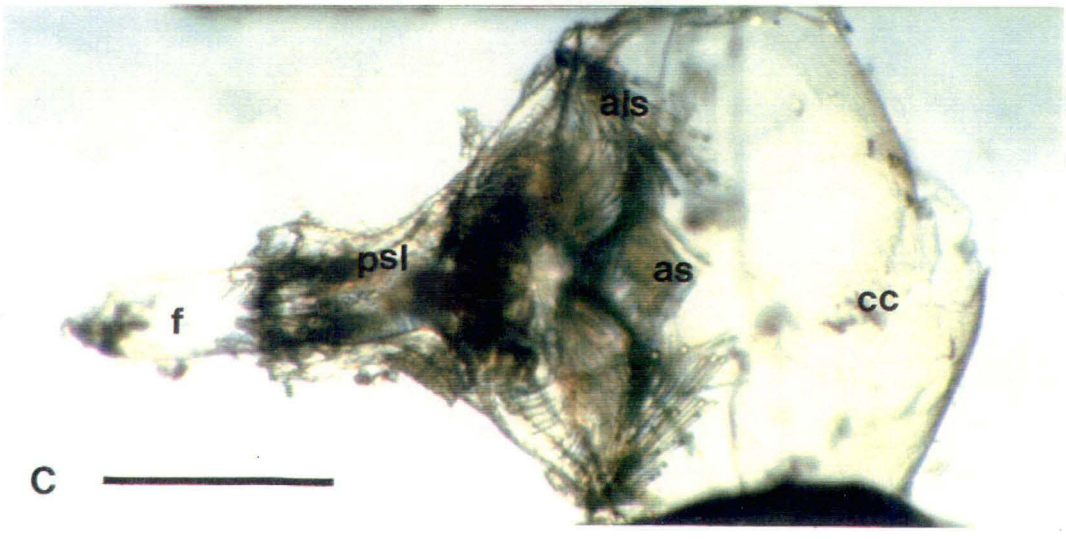
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Figure 8.12 SEM micrographs of *P. rufa* foregut. A. Anterodorsal view with dorsal wall removed showing als, am, as, cdlt, cdp, cvlt, il, pamr, pf, psl. B. Types 13, 15, 16, 17, 18 spines of cdp (right half). C. Type 10 spine. D. Right cardiac dorsolateral tooth. E. Dorsal view of right anterior laterale showing rows of types 1, 3, 4, 5 spines, and type 8 anterior laterale spine. F. Right cardiac ventrolateral tooth. G. Left cardiac ventrolateral tooth. Abbreviations as in Figure 9.10. For description of spine type see Table 9.4. Scale bar: A, D, E = 0.1 mm; B, C, F, G = 10 μm.

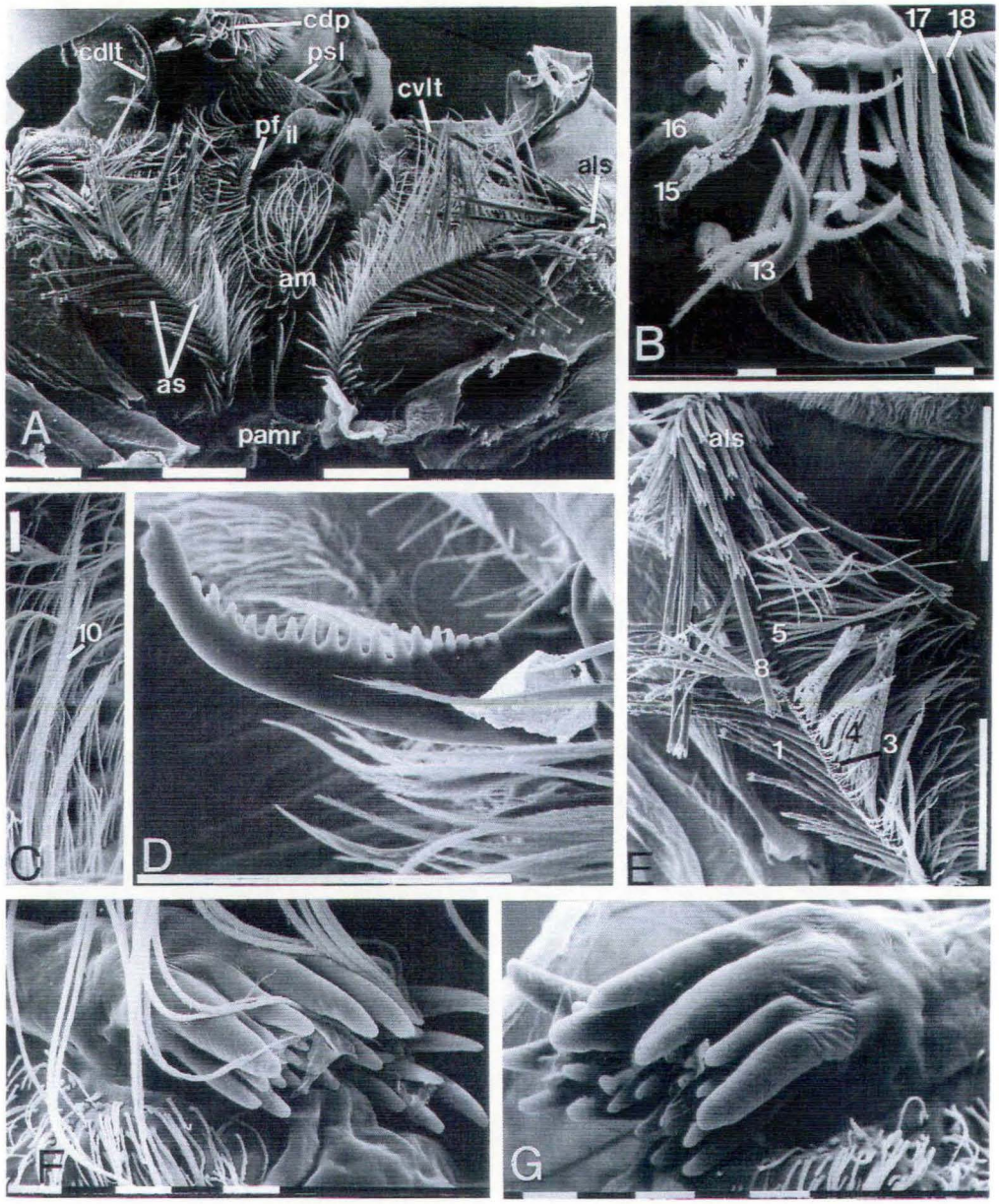
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Figure 8.13 SEM micrographs of *A. mixta australis* foregut. A. Dorsal view with dorsal wall removed showing als, am, cdlt, cdp, l, lcc, pf, and types 2 and 6 spines . B. Types 3, 4, 8, 9, and 11 spines of laterale. C. Side view of laterale showing cdlt and types 3, 4, 6 spines. D. Types 14 and 17 spines of cdp (right half), and portions of am and right cvlt. E. Left cardiac ventrolateral tooth. F. Left cardiac dorsolateral tooth. Abbreviations as in Figure 9.10. For description of spine type see Table 9.4. Scale bar: A, C = 0.1 mm; B, D, E, F = 10 μm.

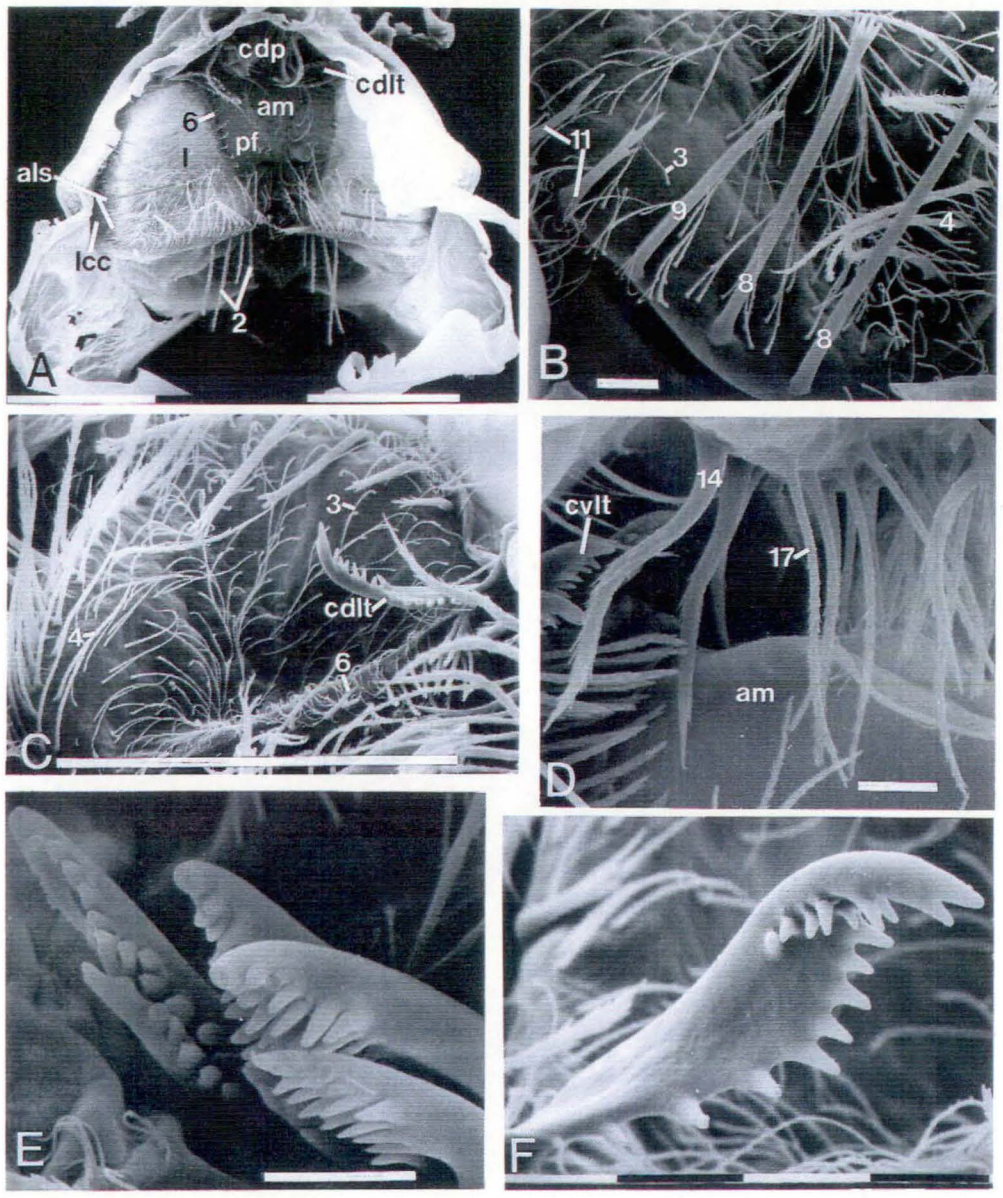
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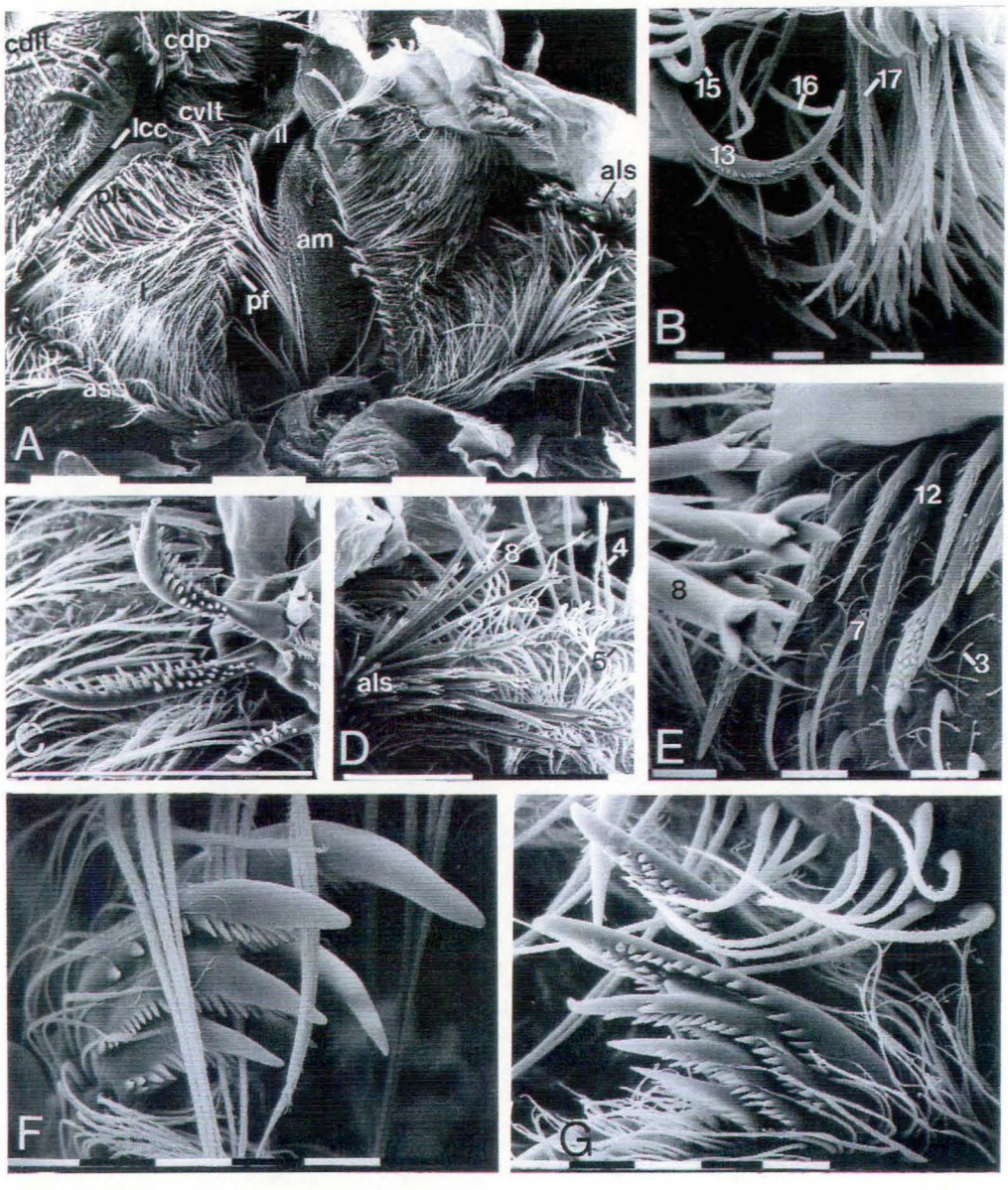
Figure 8.14 SEM micrographs of *T. tasmaniae* foregut. A. Anterodorsal view with dorsal wall removed showing als, am, as, cdlt, cdp, cvlt, il, l, lcc, pf, pls. B. Types 13, 15, 16, 17 spines of cdp (right half). C. Right cardiac dorsolateral teeth. D. Types 4 and 8 spines of laterale. E. Types 3, 7, 12 spines of laterale, and type 8 spine pronged-tips. F. Right cardiac ventrolateral tooth. G. Left cardiac ventrolateral tooth. Abbreviations as in Figure 9.10. For description of spine type see Table 9.4. Scale bar: A, C, D = 0.1 mm; B, E, F,G = 10 μm.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ridges on the ventrolateral walls of the cardiac region. Each laterale is thickest at its anterior region, and rows of spines line the margin of this region. On the ventromedial margin of the laterale a row of widely spaced and medially projecting barbed spines may be present. Underneath these spines is a row of closely spaced bristled spines, the primary filter, which separates the cardiac chamber into narrow ventral and wider dorsal food channels. The tips of the primary filter spines touch the side of the most prominent ventral ridge, the anteromedianum on the dorsal surface from which arise spines which curve posteriorly. The anteromedianum terminates at the junction between the cardiac and pyloric regions as a tongue-like structure. Grooves on the sides of the lateralia form the lateral circulation channels (these become dorsolateral in the pyloric region). The dorsolateral and ventrolateral teeth are located in the posterior cardiac region, at the cardio-pyloric junction. The ventrolateral teeth which project into the lumen of the pyloric dorsal food channel appear to dovetail each other. Dorsal to the cardiac ventrolateral teeth and slightly behind the cardiac dorsolateral teeth is the unpaired cardiac dorsal piece which comprises various spines.

The pyloric region bears prominent ventrolateral ridges called the inferolateralia which are a continuation of the ridge where the primary filter projects. The inferolateralia divide the pyloric region into a dorsal food channel, and a ventral filtration channel which communicates with the cardiac ventral filtration channels. The pyloric ventral filtration channel is separated by a prominent ventral ridge, the inferomedianum. The apex of this ridge is set out with a row of bristled spines. The inferomedianum ends posteriorly as a slender spigot. Dorsal to the inferolaterale is the pyloric superolaterale fringed by a single row of bristled spines. The walls facing the inferomedianum also bear rows of dorsomedially projecting spines. On the sides of, and running along the length of the inferomedianum are two pairs of secondary filtration channels bounded at the sides by secondary filters.

Coarse and undigested food particles are carried into the funnel region, a thin, spine-free tube which joins the anterior region of the long midgut.

Table 8.3 Size and foregut morphometrics for the three species of mysids.

	Paramesopodopsis rufa	*Anisomysis mixta australis*	*Tenagomysis tasmaniae*
Size (mean ± S.D. mm)	9.45 ± 0.42	6.08 ± 0.15	7.85 ± 0.38
Length Specific Gut Capacity (mean ± S.D. mm^2) n = 15	0.044 ± 0.005***	0.006 ± 0.001***	0.020 ± 0.003***
FGI (mean ± S.D. %) n = 15	89.6 ± 5.2^{ns}	95.0 ± 4.1^{ns}	86.8 ± 8.0^{ns}

*** highly significant difference ($p < 0.001$, Tukeys HSD Test) when compared to values from other species

^{ns} no significant difference ($p > 0.05$, Kruskal-Wallis Test) when compared to values from other species

Foregut Features in the Three Mysid Species

Paramesopodopsis rufa

The foregut of *P. rufa* has the largest length-specific volume of the three mysid species, but its FGI is not significantly different from the other two (Table 8.3). This large gut capacity is attributed to the spacious cavity formed by the anterodorsal region of the cardiac stomach (Fig. 8.11A). At the dorsal margin of the anterior laterale, four distinct rows of spines extend into the cardiac chamber (Fig. 8.12E; Table 8.4). The rake-like first row, lining the anterodorsal margin, protrudes anteriorly, and comprises type 1 spines of varying length. These spines are short at the medial base of the lateralia, but increase in length on the curvature of the anterior laterale. Those close to the side of the wall are shorter. The second row is made of type 3 spines which are curved posteriorly. Type 4 spines comprise the rake-like third row. The fourth row consists of type 5 spines which line the posterodorsal margins of the anterior lateralia. These spines are also found on the remainder of the surface of the laterale. The anterior lateral spines (ALS) appear as a cluster of type 8 spines arising from the point where

Table 8.4 Macrospines on the lateralia and the cardiac dorsal piece of the

Location	*Paramesopodopsis rufa*
anterodorsal margin of the anterior laterale	round-based, stout, stiff, distal half of shaft with sharp broad-based spinules, 3 pronged-tip (1)
	round-based, curved, thin, short, forms second row, with few minute spinules (3)
dorsal margin of the anterior laterale	flat-based, curved, with thin spinules on shaft (4)
posterodorsal margin of the anterior laterale	round-based, thin, long with fine spinules on shaft (5)
ventromedial margin of the laterale	round-based, distal half of shaft with spinules (6)
remainder of the anterior laterale	(3), (5)
anterior lateral margin of the laterale	stout, 4-7 pronged-tip with 1 central prong and the rest peripheral, spines form a cluster (8)
posterior lateral margin of the laterale	flat-based, long, stiff, with slim-based spinules on shaft (10)
cardiac dorsal piece	round-based, stout, forms J-shaped curve, with a row of spatulate spinules following curvature of shaft (13)
	as in (13), but with >1 rows of spinules on shaft (15)
	round-based, less stout, with dense fine spinules on distal half of shaft and tip (16)
	round based, thinner than (16), sparse spinulation on three quarters of shaft (17)
	round-based, thin, and short, with few alternate spinules on shaft (18)

(**Table 8.4** continuation)
foregut of three mysid species. Number in parenthesis represents type.

Anisomysis mixta australis	*Tenagomysis tasmaniae*
round-based, less stout than (1), stiff, entire shaft and tip with slim-based spinules (2)	(1)
(3)	(3)
(4)	(4)
	(4)
(6)	
only (3)	flat-based, stout, curved, with minute thin spinules (7), and (3), (5)
stout, 7 to 10 pronged-tip, prongs arranged as in (8), bifid tip (9)	(8)
round-based stout, short, pointed tip, with few sharp, slim-based spinules on shaft (11)	flat-based, robust, tooth-like pointed tip, with sharp, broad-based spinules on shaft (12)
as in (13) but less stout, with >1 rows of spinules on shaft (14)	(13), (15), (16)
(17)	(17)

the anterior laterale merge with the lateral wall of the stomach (Fig. 8.11A,B,C; Fig. 8.12A, E; Table 8.4). These spines vary in length; shorter spines surround the outer part of the cluster while those on the central portion are longer and inter-digitate with the rows of spines on the laterodorsal margin of the anterior lateralia. The surface of the remainder of the laterale bears types 3 and 5 spines (Table 8.4). The posterior lateral spines are type 10 (Fig. 8.12C; Table 8.4). On the ventromedial margin of the lateralia, several rows of type 6 spines project medially (Table 8.4).

The dorsal surface of the anteromedianum bears 25 to 30 long stout spines which are curved posteriorly (Fig. 8.12A). This patch of spines form a V-shaped pattern. The cardiac dorsolateral tooth (CDLT) projects anteromedially from a broad base (Fig. 8.12A,D). The ventral margin of the tooth is rounded and free from any dentition, while the dorsal portion is flattened and bears 11 short denticles arranged like comb blades. Distally, the rounded ventral portion becomes cylindrical, and short stout spinules are found on its dorsal surface. Just posterior to the CDLT, and before the entrance to the pyloric dorsal food channel, there is a patch of long and posteriorly directed spines. Below these spines protrudes the cardiac ventrolateral tooth (CVLT) (Fig. 8.12A,F,G). Each CVLT comprises a cluster of 20-22 smooth and finger-like spines.

The cardiac dorsal piece (CDP), which is basically a group of spines hanging from a ridge in the roof of the cardio-pyloric junction, lies between the pair of cardiac dorsolateral teeth (Fig. 8.12A). The CDP comprises types 13, 15, 16, 17, and 18 spines (Figure 8.12B).

Anisomysis mixta australis

Although *A. mixta australis* showed the smallest gut volume, its FGI is similar to those in the other two species (Table 8.3). Like the other two species, the anterior surface of the laterale is bare, but four type 2 spines project on its anterodorsal margin (Fig. 8.13A; Table 8.4). A posterior second row of type 3 spines is also present (Fig. 8.13B, C; Table 8.4). Next to the second row, on the posterior surface of the margin, is the third row of type 4 spines (Fig. 8.13B, C; Table 8.4). The

remainder of the surface of the laterale, except its ventral and dorsolateral margins, is sparsely covered only with type 3 spines (Fig. 8.13C). The lateral margins of the laterale bear two pairs of type 8 spines as their anterior lateral spines (ALS). These spines are longer than the two pairs of type 11 and a pair of type 9 posterior lateral spines (PLS) that are also present (Fig. 8.13B; Table 8.4). Although these spines resemble those found on the ALS of *P. rufa* and *T. tasmaniae*, they are isolated and do not form a cluster. The ventromedial margin of the lateralia possesses a widely spaced row of type 6 spines (Fig. 8.13A,C; Table 8.4).

Sixteen long stout spines which are curved posteriorly adorn the dorsal median region of the anteromedianum (Fig. 8.13A). Like in *P. rufa*, these spines form a V-shaped pattern of distribution. The stout and curved cardiac dorsolateral tooth (CDLT) projects anteromedially above the posterior region of the anteromedianum (Fig. 8.13A,C,F). Both CDLT extending from the dorsal wall of the stomach are arranged symmetrically. Each tooth is fringed with small blunt teeth (Fig. 8.12F). Between 19 to 21 small denticles are present, but only on the margins and on the distal portion of the tooth. The cardiac ventrolateral tooth (CVLT) is formed by a cluster of barbed spines (Fig. 8.13D,E). Five stout spines form the cluster, and each of the 3 more dorsal spines is endowed with broad-based blunt denticles on the ventral surface of the shaft.

The cardiac dorsal piece (CDP) consists only of type 14 spines on its side and type 17 spines in the middle (Fig. 8.13D; Table 8.4).

Tenagomysis tasmaniae

The foregut volume of *T. tasmaniae* is almost half the value measured in *P. rufa*, while its FGI is similar to that of the other two species (Table 8.3). As in *P. rufa*, the anterodorsal and dorsal margin of the anterior lateralia possesses four rows of similar types of spines (Table 8.4). The posterodorsal margin bears type 4 spines (Fig. 8.14D). The remainder of the surface of the laterale comprises types 3, 7 (Fig. 8.14E; Table 8.4) and 5 (Fig. 8.14D) spines. Although the tips of the anterior lateral spines (ALS) appear sharper in *T. tasmaniae*, the structure and arrangement of the ALS are

very similar to those in *P. rufa* (Fig. 8.14A,D). The posterior lateral spines consist of a pointed, robust and sharply-barbed type 12 spine (Fig. 8.14E; Table 8.4). In *T. tasmaniae*, the ventromedial margin of the lateralia bears no type 6 spines which are present in the other two species.

The anteromedianum, distinct in *T. tasmaniae*, has a pointed apex and a narrower base (Fig. 8.14A). In contrast, in the other two species, the anteromedianum is almost dome-shaped and has a broad base. The anterior three quarters of the anteromedianum's pinnacle bears a row of 17 long bristled spines which curve posteriorly. Three symmetrical pairs of cardiac dorsolateral teeth (CDLT) are present (Fig. 8.14A,C). The two anterior teeth are larger than the more posterior tooth. The teeth are prominent processes dorsal to the lateral circulation channel. Rows of very sharp denticles arm the dorsal surface of each tooth. The cardiac ventrolateral teeth (CVLT) of *T. tasmaniae* appear as a cluster of seven saw-like spines (Fig. 8.14A,F,G).

The cardiac dorsal piece (CDP) in *T. tasmaniae* closely resembles that of *P. rufa* (Fig. 8.14A,B) The structure is also composed of types 13, 15, 16, and 17 spines (Fig. 8.14B).

Discussion

Comparative Morphology of the Thoracic Endopods and Mouthparts

The Endopods

The endopods of the three mysid are similar, and are consistent with those described in the majority of mysid species (Tattersall and Tattersall 1951; Mauchline 1980). All three have a terminal sharp spine or nail and serrated setae, which contribute to grasping large food particles. In oceanic genera such as *Eucopia* and *Hansenomysis*, the terminal nail and one or more setae on some endopods form a pseudochela which increases grasping efficiency (Mauchline 1980).

Setal types found on the endopods of the three species are similar to the types of setae in *Antromysis juberthiei* (Crouau 1989) and those in *Mysis relicta* (Sierszen *et al.* 1982). The setae possess setules on the proximal regions of their shafts and sharp tips which may function both for capturing small and large particles (Gauld 1966 cited in Tiselius and Jonsson 1990). Crouau (1989) has identified chemosensory, mechanosensory, and chemo-mechanosensory types. Serrated types of setae may be associated with grooming function (Acosta and Poirrier 1990). These cuticular projections may also be involved in increasing the efficiency of capturing microscopic and macroscopic potential food particles (Mauchline 1980; Webb and Wooldridge 1989; Sierszen *et al.* 1982). The cleaning mechanism structures on the endopods may have a role in crustacean feeding (Robertson and Mann 1980).

Although the mechanical sieve hypothesis for the feeding appendages in suspension feeding crustaceans has been discredited as a poor predictor of the size range of food particles by several studies (Donaghay and Small 1979, Vanderploeg 1981; Vanderploeg and Ondricek-Falscheer 1986; Donaghay1988), data from mesh size ranges could not be entirely considered useless nor the hypothesis entirely rejected (McClatchie and Boyd 1983). Aside from Boyd (1976), several more recent studies performed on calanoid copepods and in other crustaceans, support the hypothesis but only within a modified conceptual framework. Intersetal or intersetular gap measurements are usually made on the assumption that setules and setae are stiff and immovable structures. This is absolutely not the case as feeding appendages from which these bristles arise are movable, therefore intersetal gaps depend on the orientation and overall behaviour of these limbs (Vanderploeg 1990). Movements and orientation in space of the different feeding limbs affect the actual efficiency of the different setal and setular projections (Strickler 1984; Vanderploeg 1990). Nevertheless, the data presented here would still provide relevant information on the potential sizes of food particles suspension feeding crustaceans may be capable of capturing. From micro-videographic observations (chapter 2), outstretched endopods have their component segments twisted close to 90° posteriorly resulting in the tips of their setae touching the setae-free shaft of the next more posterior endopod. This

orientation of the setae could capture a range of particle sizes of potential food not necessarily reflected by the intersetal gaps.

The intersetal gap range of 8-118 μm reported here does not necessarily suggest capture of food particles which fall within this range. The three mysid species are, indeed, capable of capturing food particles larger than 118 μm through the raptorial mode. Capture of large size particles may be limited by the maximum allowable span of the endopods. The intersetal gaps reported may be best related to capture of finer food particle. Body size appears to be related to intersetular gap measurement. The smallest species, *A. mixta australis* showed no intersetal gaps > 96 μm indicating that this species may be efficient in capturing much finer sizes of food particles. The medium size species, *T. tasmaniae*, also seems better equipped for capturing finer particles as indicated by comparable frequency of smaller intersetal gaps to those in *A. mixta australis*. However, the comparable frequency of the much wider gaps to those in *P. rufa* also suggests probable efficiency for large sized particles. The largest species, *P. rufa* may show reduced efficiency in capturing very small particles, but seems to be well suited to capturing larger particles.

The Mouthparts

The basic form of the mouthparts of the three mysid species is similar to those described in the majority of mysid species by Mauchline (1980). The most anterior, the upper lip or the labrum, does not show distinct modification in the three mysid species. In addition to swinging forward allowing the mandibles to perform their latero-ventral food-processing movements, the labrum in mysids also acts as an anterior boundary of the buccal cavity and prevents ingested food from falling ventrally (Hassal 1977; Mauchline 1980, 1989). The flap in contact with the paragnaths of the labium is fringed with spines which may serve to fix food in place. These spinous structures are similar in form and disposition and may not indicate specialized function or a particular feeding habit.

The symmetrical labium or lower lip and its ventrally projecting paragnaths is similar in the three mysid species and those in other species (Mauchline 1980). The

fact that these structures can move laterally to a limited degree as noted in euphausiids (Mauchline 1989), they may also aid in holding particles being ingested or for large particles chewed by the *pars incisiva* of the mandibles. During mandibular chewing, the meshing on the paragnaths may also prevent loss of colloidal and particulate organic carbon as indicated in *Mysis relicta* (Sierszen 1982). In euphausiids, this meshing can actually remove food from the filtering setae and spines on the lobes of the maxillules and maxillae (Mauchline 1989).

The mandibular palps, joined at the anterior aspect of the body of the mandibles, are directed anteriorly and adpressed against the ventral base of the antennae. The palps of the three mysid species are similar to those of *Schistomysis ornata* described by Mauchline (1980). The palps remove food from the posterior mouthparts and push it into the mouth (Mauchline 1980). The mandibular palps in Euphausiacea are very similar in disposition and form to those in Mysidacea, and Mauchline (1989) noted that in euphausiids, the palps aid in transferring food from the mouthparts to the oral cavity. Palps with elaborate setation have been associated with herbivorous feeding in euphausiids (Mauchline 1980, 1989) and in caprellid amphipods (Caine 1974). This structure may be reduced or absent in predatory amphipod and euphausiid species.

Itoh's (1970) edge index is not directly applicable in Euphausicea and Mysidacea because copepod mandibles differ from those in the two groups (Mauchline 1980). Nemoto (1977) developed an edge index for euphausiids which, according to Mauchline (1980), is also applicable in mysids. McClatchie and Boyd (1983) have shown that in the primarily herbivorous species, *Euphausia superba*, apart from having a large *pars molaris*, it is also endowed with specialized surfaces that can split diatom chains, cut or fracture hard tests, and grind particles smaller than 10 μm. Mauchline (1980) noted that the deep sea lophogastrid mysids possess large *pars molaris* suggesting herbivory; their habit of vertically migrating to shallower regions at night to forage on diatomaceous phytoplankton may explain the use of a large grinding region in their mandibles.

The mandibular edge index measurements suggest differences in the feeding habits of the three mysid species. The smallest *pars molaris* was shown by *P. rufa*, and *T. tasmaniae* had the largest. The mandibular edge indices shown by the three mysid species agree with the predominant dietary items (Fenton 1986). *P. rufa*, with the lowest mandibular edge index, fed more on crustaceans while *T. tasmaniae*, with the largest index fed largely on algal detritus. It is interesting to note that *A. mixta australis* with a median edge index fed mostly on finer particulate food materials. Its higher edge index value than that in *P. rufa* suggests feeding habits similar to that in *T. tasmaniae*. However, it is too simplistic to interpret feeding habits from features of the mandibles alone. For instance, the mandibular edge index of the euphausiid *Nyctiphanes australis* suggested a carnivorous feeding habit, however mandibular palp length suggest herbivory (Dalley and McClatchie 1989). This euphausiid species has been regarded as an opportunistic omnivore from morphological and gut content evidence. The orientation and disposition of the *lacinia mobilis* and spine rows of the mysids in the present study are similar in the two large species indicating similar masticating function. However, in *A. mixta australis*, blunt spines on the *lacinia* and thin spines comprising the spine row may function best for softer and finer food particles. The functions of the *lacinia mobilis* in Peracaridan mandibles include biting, cutting, guiding the *pars incisiva* into right planes and position, and holding food particles during the bite (Dahl and Hessler 1982; Watling 1993). The three mysid species possess pores on the edges of their *pars molaris*. These pores may function in contact chemoreception as noted in copepods (Friedman 1980) and in *Artemia* (Mura and del Caldo 1992).

The maxillules are considered the most constant mouthpart in form and probably in function, however differences were found between the three species. The number of stout and barbed spines on the distal lobe or endite varies considerably. The smallest species, *A. mixta australis* bears the lowest number of these spines, while *T. tasmaniae* has the highest number. Another difference is in the shape of these biting spines: *T. tasmaniae* has sharp tips suggesting greater efficiency in containing or holding food particles. In contrast, *P. rufa* and *A. mixta australis* have more blunt

spines similar to those shown in *Antromysis juberthei* (Crouau 1989). The differences in the spine shape may be a function of the size of the species and the quality of food the three species process. *A. mixta australis* could manipulate smaller food than the two larger species.

The maxilla of the three species is similar to the phyllopodan type of crustacean appendage (McLaughlin 1982). Features which differ markedly between the three species include the number and type of setae on the inner margin of the proximal and distal endites, and the margin of the maxillary palps. In terms of number and type of setae, the two larger species, *P. rufa* and *T. tasmaniae* show close resemblance in that they possess denser plumose and strongly serrated types than in *A. mixta australis*. This may be because *A. mixta australis* is small in size and prefers small or softer types of food (perhaps from scavenging) which do not require powerful setation. In contrast, the two larger species feed on a much broader range of food particles, with particular emphasis on large size. These larger species could be differentiated by the type of setae on the apical margin of the maxillary palp. *T. tasmaniae* bears strongly serrated and sharp-tipped setae which may help push and contain coarse and tough food materials to the entrance of the mouth. These setae are unusual in the genus although all Tasmanian *Tenagomysis* have them (Fenton 1992). This type of seta, in conjunction with similar types of setae found on the dactyli of the first and second maxillipeds, may explain the observed habit of rolling sand grains against these mouthparts as a method of removing organic materials that coat these particles. This may not be shown in the other two species which bear simple plumose and lightly serrated setae on their maxillary palps.

The first and second endopods are not strictly defined as maxillipeds because of the presence of exopods (Mauchline 1980; Crouau 1989). However, morphological and functional evidence shown in this study strongly supports naming the first two thoracic endopods as maxillipeds. The disposition and arrangements of the two limbs agrees with the description by Cannon and Manton (1927). Observations from suspension and predatory feeding mechanisms in the three species have revealed the food handling and manipulating function of the maxillipeds or first

and second endopods (E1 and E2) (Chapter 2). Variable density of setae distributed on the medial surfaces of the different podomeres of the maxillipeds I is shown in the three mysid species. *A. mixta australis* has fewer and less powerful setae than the other two larger species. This may be related to its preference for small sized and softer food particles. However, *A. mixta australis* possesses a very sharp spine on the dactylus of its first maxilliped, a feature present in *P. rufa* but absent in *T. tasmaniae*. By virtue of this robust spine, *A. mixta australis* and *P. rufa* may show a greater efficiency than *T. tasmaniae* in immobilizing and restraining animal prey. The strongly serrated, curved and sharp setae of the latter species are efficient in dealing with food materials such as algal detritus and in scraping from hard surfaces.

The maxillipeds II are similar in the three species, but specializations were also observed. Only *T. tasmaniae* showed closely gapped serrated setae on the maxilliped dactylus and extensive and closely-spaced setae on the medial surface of the pre-ischium of maxillipeds II. This further supports the idea that this species is more capable of processing and manipulating tough and coarse food particles. The dactyli of the maxillipeds II of both *A. mixta australis* and *P. rufa* have a robust spine suggesting that they are more efficient manipulators of animal prey. The pre-ischia of these two latter species bear widely-spaced setae.

Comparative Morphology of the Foregut

It is widely recognised that the gross structure of mysid foreguts is similar to the eucaridan (Euphausiacea and Decapoda) proventriculus or gastric mill (Gelderd 1909; Haffer 1965; Mauchline 1980; Fretter and Graham 1976; Storch 1989; Ullrich *et al.* 1991), and to the foregut of other peracarids (*e.g.* Storch 1987, isopod; Icely and Nott 1984, amphipod). These similar features are shared by the three mysid species examined here, but apparent differences are also observed. These differences in structure and probable function, and the possible evolutionary feeding lines are summarized in Table 8.5.

Table 8.5 Foregut features and their probable function (in parentheses),

	Paramesopodopsis rufa
Spination Pattern on Lateralia	
anterior margin	> 1 rows of both stout (prong tipped) and thin spines (raking large clumps of food from anterior to posterior chamber)
remainder of the surface	dense and different types (pushing large bulky food)
anterior lateral spines (ALS)	clustered with pronged tips (pushing, cutting, shearing large food particles)
Cardiac Dorsal Piece (CDP)	more spines of the stout curved type (type 16) (pushing larger food mass into posterior foregut)
Cardiac Dorsolateral Teeth (CDLT)	as in *A. mixta australis*
Cardiac Ventrolateral Teeth (CVLT)	clustered with no dentition (squeezing and grinding)
Possible Evolutionary Feeding Line (after Kunze and Anderson 1979)	Type Ib: predominantly macrophagous (mainly predatory, necrophagous, detritivorous)

(**Table 8.5** continuation)

and possible feeding adaptations of three mysid species.

Anisomysis mixta australis	*Tenagomysis tasmaniae*
single row of thin spines (pushing finer and softer food particles)	as in *P. rufa*
only type 3 spines (pushing finer and softer food)	denser and more diverse than in *P. rufa*; spine types with sharp cusps (pushing and shearing large bulky food)
spines isolated and few (pushing and shearing smaller food particles)	clustered with pronged tips (as in *P. rufa* but possibly more powerful)
few spines without the stout curved type (pushing smaller food mass into posterior foregut)	as in *P. rufa*
single with few blunt cusps (transporting clumps of food; limited cutting function)	three with many sharp cusps (cutting and transporting clumps of food)
clustered with blunt dentition (squeezing, grinding and some degree of cutting)	clustered with sharp dentition (squeezing, piercing, grinding and cutting)
Type Ia: predominantly microphagous (mainly feeds on fine particulate matter)	Type Ic: predominantly macrophagous (mainly feeds on tough plant detritus)

Storch (1989) noted that cuticular projections on the lateralia may act to push the food posteriorly. The series of rows of spines cannot be interpreted as a passive sieve (Nath and Pillai 1973) because the action of the intrinsic and extrinsic muscles associated with the lateralia would certainly impart active movements to these structures. Activity of these structures is likely to keep coarser food particles in the dorsal region of the cardiac stomach, and the finer particles in the ventral region (Storch 1989). As well as aiding the rows of spines on the margin of the anterior lateralia in translocating large and bulky food from the anterior cardiac chamber, the anterior lateral spines (ALS) may also press the food mass against the primary filter for the initial straining. Furthermore, they dovetail to each other, and in the process of pressing, individual spines probably exert a shearing action. In this manner, some food components may be ground into a pulpy consistency. Coordinated by extrinsic and intrinsic muscle contraction (Haffer 1965), the ALS may also push the food towards the cardio-pyloric junction where food is further processed by the cusped cardiac dorsolateral teeth (CDLT) and ventrolateral teeth (CVLT). The cardiac dorsal piece (CDP) has been suggested to push food masses into the more posterior region of the foregut (Storch 1989).

Fretter and Graham (1976) suggested that tooth-bearing ridges at the junction between the cardiac and pyloric chambers process the food, keep coarser food particles away from the ventral passages of the pyloric chamber, and regulate passage towards the midgut. The CDLT and CVLT are found in the region of the foregut where a prominent set of extrinsic muscles originates (Haffer 1965). The action of these muscles moves these teeth, and depending on the integrity of these structures, therefore also the food-processing action. Ullrich *et al.* (1991) have noted that in *Euphausia superba*, the foregut regions, where the lateral teeth and cluster spines are associated (structures possibly homologous to the CDLT and CVLT in mysids), display activities that indicate a crushing and triturating function.

The differences in gut volume of the three species indicate another possible adaptation to diet. The FGI developed by Suh and Nemoto (1988) seems to obscure the apparent function of the foregut, particularly the cardiac chamber, because it does

not take into account its three dimensional nature. *P. rufa*, the primarily carnivorous species, has the largest length-specific gut volume, while the primarily fine particulate feeder *A. mixta australis*, (due to size) showed the smallest volume; and *T. tasmaniae*, the algal detritus feeder, showed gut volumes half those of *P. rufa*. Studies on other peracarids have shown that the foreguts of mainly carnivorous-necrophagous species differ from those of mainly herbivorous or detritivorous species by having large volumes which have been suggested as an adaptation to storing large and soft food materials typical of animal prey only present for short periods (*e.g.* Jones 1968; Keith 1974; Sheader and Evans 1975; Hassal 1977; Icely and Nott 1984). Similar observations have been noted by Nemoto (1977) in the bathypelagic carnivorous thysanopod euphausiids. The elaborate distribution of spines in *T. tasmaniae* (relatively detritivorous) and a relatively small gut capacity may be associated with the rapid removal of macrophyte detritus (less nutritious) from the gut (Calow 1981; Zagursky and Feller 1985). Aside from food particle size, the availability, diversity, and nutritional value are also manifested in gut structure (Icely and Nott 1984).

In euphausiids, internal gut armature may be more taxonomically rather than diet related (Suh and Nemoto 1988; Suh 1990). The digestive system of other decapods depends primarily on the phylogenetic history of the species, but can be modified partially by other factors such as diet (Kunze 1981; Icely and Nott 1992). The three mysid species belong to the same Sub-Family (Mysinae) (Fenton 1986), and although they belong to different Tribes (both *P. rufa* and *A. mixta australis* belong to the same Tribe Mysini while *T. Tasmaniae* belongs to the Tribe Leptomysini) some foregut features are similar in both Tribes and some features are not shared within Tribes (see Table 8.5). Phylogenetic history, in the present context, is weak in explaining the differences in foregut armature. To my knowledge, this is the first comparative study on the fine foregut structure of mysids with known diet, and the features of the internal gut armature shown by the three species are in keeping with the theory that the feeding apparatus is adapted to cope with the various types of food resource utilised by the animal (Fryer 1977; Dahl 1979; Icely and Nott 1992). In the next chapter, the importance of foregut phylogeny and feeding adaptations are

explored in the three mysid species together with other co-occcurring mysids from different biogeographical zones of the globe.

Species with similar trophic ecologies may coexist by partitioning of feeding niche as indicated by differences in feeding structures (Schoener 1974). Webb and Wooldridge (1989) noted that the differences in gut armatures allow two co-occurring mysid species to utilize overlapping portions of the food resource. Icely and Nott (1992) suggested that subtle modifications in the gastric mill allowed four closely related species of fiddler crabs to cohabit by specializing in different niches. Aside from habitat and food resource partitioning (Fenton 1986), the morphological evidence presented here may also help to explain the co-occurrence of these three mysid species.

CHAPTER 9

COMPARATIVE MYSID FOREGUT MORPHOLOGY

Introduction

Studies on the morphology of the crustacean foregut are often aimed at unravelling the diversity of form and structure and to deduce the possible functions. For example, the basic foregut structure of adult decapods consists of a complete set of ossicles and a well developed gastric mill (Felgenhauer and Abele 1989). Because of the strong resemblance in morphology of the different species examined despite their difference in ecological habits, the basic structure of the decapod foregut is probably determined by phylogeny (Felgenhauer and Abele 1989). However, there is also strong evidence on the importance of diet, for example, examination of the foregut and mouthparts of seven species of anomurans led Caine (1975) to conclude that the effect of diet appears to be more important than phylogeny. Kunze and Anderson (1977) suggested microphagous (filter feeding) and macrophagous (predation on large food masses) evolutionary feeding lines in three anomurans. Icely and Nott (1992) as already mentioned in chapter 8 noted that four closely-related fiddler crabs co-exist partly because of the subtle modifications in their gastric mill allowing them to specialize on different feeding habits.

In euphausiids, the cardiac part of the foregut is either expanded and swollen or slender and less swollen, features which according to Nemoto (1977) are related to carnivorous and herbivorous feeding, respectively. Suh and Nemoto (1988), however, argued that because of the striking similarity of the foregut shape and internal armatures of 10 species, foregut morphology is more related to phylogeny than to diet. These authors categorized these species on the basis of having the secondary filter or not, and on the structures of the gastric mill. Three categories were proposed, namely those with the filter press (Group I, represented by a single species *Bentheuphausia amblyops*), those without the filter but with an elaborate gastric mill

(Group II represented by most species analyzed), and those without the filter and lacking the lateral teeth (Group III represented by the deep sea species of *Thysanopoda*, and the genera *Nematobrachion*, and *Stylocheiron*, taxa regarded by Nemoto (1977) as highly carnivorous). Recently, Suh (1990) noted that the thysanopod euphausiids may be the point of divergence among euphausiids because of the presence of foregut types belonging to Groups II and III.

As further examples, Kunze (1981) noted that the Peracarida exhibit a diversity of modifications of the foregut which partly reflect diet but which also reflect divergent trends in adaptive radiations. The amphipodan foregut follows the trend of having complex gastric armatures as represented by species in the Order Gammaridea and those in the Family Caprellidae (Order Caprellidea), to the loss of structures and secondary filter system as represented by species belonging to the Family Cyamidae (Order Caprellidea) (Icely and Nott 1984). These authors further noted that the relatively complex gut in the Gammaridea and Caprellidae enables the animals to extract nutrients from bulky food of relatively poor nutritional value in comparison with the simple and reduced gut of the parasitic cyamids and some hyperiids. The enlarged stomach and anterior intestine of the carnivorous hyperiid *Parathemisto gaudichaudi* are adaptations for prey or food storage (Sheader and Evans 1975). Coleman (1994) examined several hyperiid species, and noted that the trend includes a reduced and even the loss of filter capability, some filtering device present but of different origin, and the stomach cavity greatly reduced relative to the size of the midgut gland or hepatopancreas. In the last category, the midgut gland has become a series of sac-like digestion chambers deviating from the ancestral blind-ending tubes. Coleman (1994) suggested that the reason for this trend may be the main diet of hyperiid species, *i.e.* soft bodied prey, or the necrophagous feeding habit. Likewise, Oshel and Steele (1988) stated that the reduction and simplification of the lateral ampullae in the foreguts of gammaridean amphipods may be correlated with a trend from detritivorous and/or scavenging diet to necrophagous diet.

The divergence from omnivorous to carnivorous condition in Isopoda is associated with the reduced size and the absence of grinding plates and filtering

apparatus of the cardiac region (Jones 1968). Strong and complex gut armatures (Hassal and Jennings 1975; Hassal 1977) and lead encrustations on the ridges of the cardiac chamber (Storch 1987) have evolved to effectively translocate and to some degree masticate cellulose-based food items in the predominantly detritivorous terrestrial isopods.

Apart from the present investigation, no mysid foregut morphology study has taken a similar theoretical approach, though Webb and Wooldridge (1989) suggested that the differences in the foregut morphology in two coexisting South African mysid species (re-examined here) is mainly due to diet.

Whether phylogenetic history rather than diet is best reflected in crustacean foregut morphology is a matter of debate, but it is reasonable to accept the inter-relatedness of adaptation and phylogeny. Coleman (1994) noted that differences in food preference and systematic positions are the main reasons for the differences in development and morphology of foregut structures. Harvey and Pagel (1991) stressed that closely related species will have genes in common through descent from common ancestors and are likely to be more similar in both phenotype and lifestyle than distant relatives. They also stress the need for the study of comparative trends together with phylogenetic relatedness.

In this chapter the foreguts of co-existing and single mysid species from different geographic locations were surveyed, and a phylogenetic relationship based on foregut morphology is proposed. These data are used to test the hypothesis outlined in chapter 8 that diet exerts a strong influence on the foregut morphology of mysids.

Materials and Methods

Source of Material

Forty eight species including the three from southeast Tasmania were analyzed in the present study (geographic locations in Fig. 9.1; list in Table 9.1).

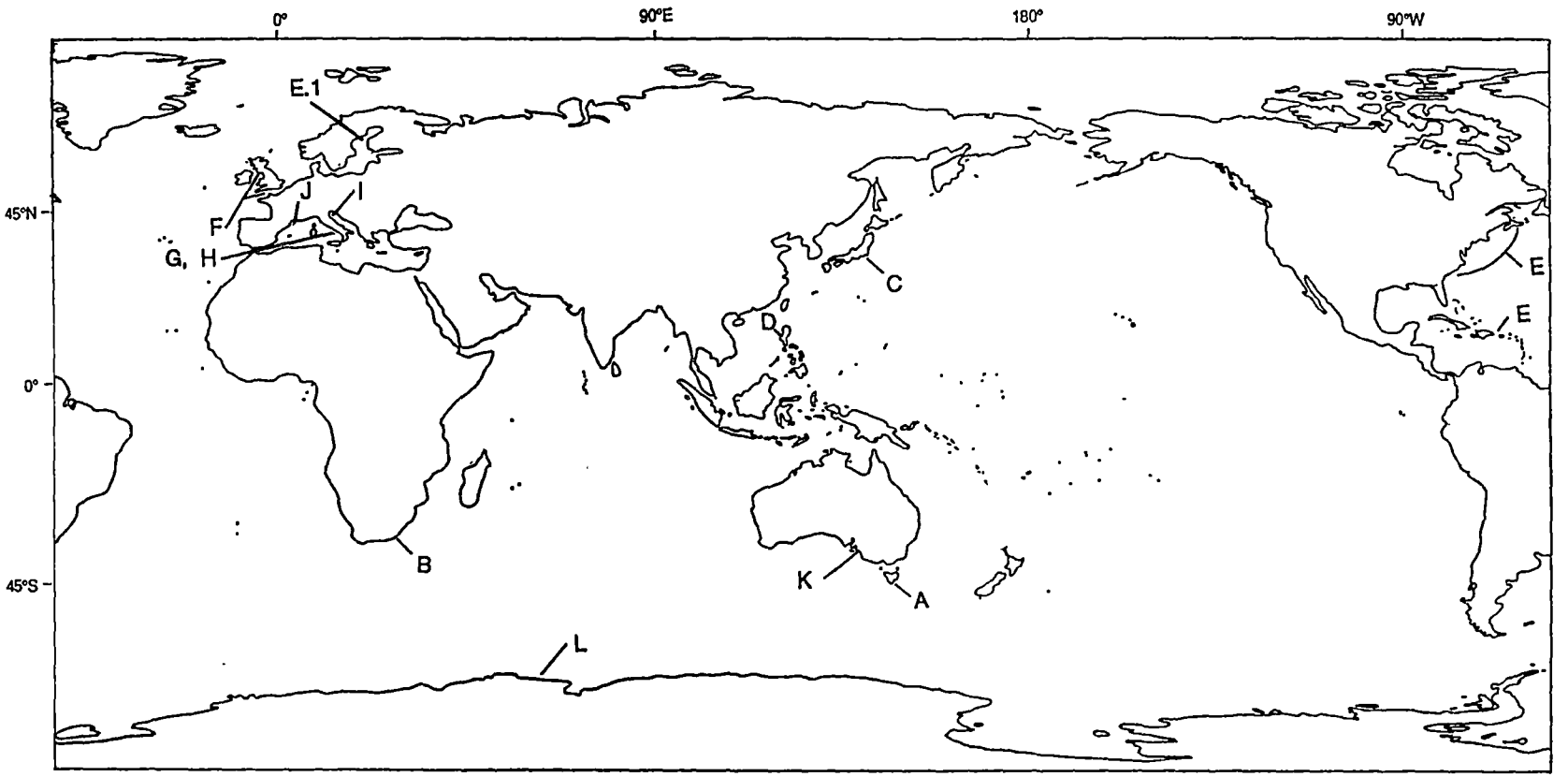

Figure 9.1 Geographic locations of the sources of mysid specimens analyzed in the present study. A. Derwent Estuary, Southeast Tasmania. B. Algoa Bay, South Africa. C. Off Tateyama, Central Japan. D. Off Bolinao, Northwest Philippines. E. East Coast, USA and Puerto Rico. E.1. Norther Baltic Proper. F. Off Argyll, Scotland and English Channel. G., H. - Gulf of Naples and Gulf of Salerno, Tyrrhenian Sea. I. North Adriatic Sea. J. Gulf de Marseille, France. K. False West Bay, South Australia. L. Off Mawson, Antarctica.

Table 9.1 Localities, depth and salinity of the mysid species analyzed.

Species	Locality
Anisomysis mixta australis	Off Taroona Beach, Taroona, Southeast Tasmania
Paramesopodopsis rufa	Off Taroona Beach, Taroona, Southeast Tasmania
Tenagomysis tasmaniae	Off Taroona Beach, Taroona, Southeast Tasmania
Tenagomysis australis	Off Taroona Beach, Taroona, Southeast Tasmania
Tasmanomysis oculata	Off One Tree Point, Bruny Island, SE Tasmania
Australomysis acuta	Off One Tree Point, Bruny Island, SE Tasmania
Rhopalophthalmus terranatalis	Sundays River Estuary, Algoa Bay, South Africa
Gastrosaccus brevifissura	Sundays River Estuary, Algoa Bay, South Africa
Gastrosaccus psammodytes	Sundays River Beach, Algoa Bay, South Africa
Mesopodopsis wooldridgei	Sundays River Estuary, Algoa Bay, South Africa
Anisomysis ijimai	Off Banda Beach, Tateyama, East Central Japan
Nipponomysis lingvura	Off Banda Beach, Tateyama, East Central Japan
Siriella longipes	Off Banda Beach, Tateyama, East Central Japan
Gastrosaccus bengalensis	Off Santiago Island, Bolinao, Northwest Philippines
Siriella anomala	Off Santiago Island, Bolinao, Northwest Philippines
Anchialina typica	Luispena Channel, Puerto Rico
Mysis stenolepis	Off South Harpswell, Casco Bay, Maine
Mysis mixta	Northern Baltic Proper, Sweden; Off Eastport, Maine
Bowmaniella brasiliensis	Indian River Inlet, Delaware
Mysidopsis bigelowi	Indian River Inlet, Delaware
Erythrops erythrophthalma	Massachusetts Bay, Massachusetts
Neomysis americana	York River Estuary, West Point, Virginia
Neomysis integer	Loch Creran, Argyll, Scotland
Praunus flexuosus	Firth of Lorn, Canavan Bay, Argyll, Scotland
Praunus neglectus	Roscoff, English Channel
Paramysis nouveli	Roscoff, English Channel
Leptomysis gracilis	Punta Revellata, Corseca
Leptomysis lingvura marioni	Gulf of Naples, Italy, Tyrrhenian Sea
Leptomysis posidoniae	Gulf of Naples, Italy, Tyrrhenian Sea
Pyroleptomysis rubra	Gulf of Naples, Italy, Tyrrhenian Sea
Siriella clausii	Gulf of Naples, Italy, Tyrrenian Sea
Siriella jaltensis gracilipes	Gulf of Naples, Italy, Tyrrhenian Sea
Mysidopsis gibbosa	Gulf of Naples, Italy, Tyrrhenian Sea
Hemimysis lamornae mediterranea	Gulf of Naples, Italy, Tyrrhenian Sea
Gastrosaccus sanctus	Gulf of Salerno, Italy, Tyrrhenian Sea
Schistomysis assimilis	Gulf of Salerno, Italy, Tyrrhenian Sea
Haplostylus bacescui	Gulf of Salerno, Italy, Tyrrhenian Sea
Haplostylus normani	Gulf of Salerno, Italy, Tyrrhenian Sea
Paramysis arenosa	Gulf of Salerno, Italy, Tyrrhenian Sea
Leptomysis buergii	Off Near Rovinj, Croatia, Adriatic Sea
Leptomysis lingvura adriatica	Bay of Strunjan, Adriatic Sea
Siriella armata	Bay of Strunjan, Adriatic Sea
Acanthomysis longicornis	Bay of Strunjan, Adriatic Sea
Mesopodopsis slabberi	Bay of Strunjan, Adriatic Sea
Hemimysis speluncula	Gulf de Marseille, France
Gastrosaccus indicus	False Bay West, South Australia
Antarctomysis maxima	Off Mawson, Antarctica
Limnomysis benedeni	Lake Balaton, Hungary

Table 9.1 Continuation

Greenwich Coordinates	Depth (m)	Salinity (‰)
42° 57' S, 147° 21' E	0.5 - 3	30 - 35
42° 57' S, 147° 21' E	0.5 - 3	30 - 35
42° 57' S, 147° 21' E	0.5 - 3	30 - 35
42° 57' S, 147° 21' E	0 - 2	30 - 35
43° 5' S, 147° 22.5' E	1.2 - 6	30 - 35
43° 5' S, 147° 22.5' E	0.3 - 7	30 - 35
26° 41.2' S, 25° 51.56' E	< 2 - 6	10 - 34
26° 41.2' S, 25° 51.56' E	< 2 - 6	10 - 34
26° 41.2' S, 25° 51.56' E	0 - 4	10 - 34
26° 41.2' S, 25° 51.56' E	< 2 - 10	10 - 34
34° 59' N, 139° 50' E	0.5 - 8	30 - 34
34° 59' N, 139° 50' E	0.5 - 8	30 - 34
34° 59' N, 139° 50' E	0.5 - 8	30 - 34
16.25 ° N, 119.50° E	0 - 5	34 - 35
16.25 ° N, 119.50° E	0 - 5	34 - 35
18.5° N, 65.5° W	32 - 38	31 - 33
44.75° N, 70.12° W	0 - 5	31 - 33
58° 50' N, 17° 40' W; 44.88° N, 67.21° W	20 - 40	31 - 33
39° 30' N, 75° 37.5' W	<10	31 - 33
39° 30' N, 75° 37.5' W	13 - 179	31 - 33
41° 58' N, 70° 21' W	60 - 117	31 - 33
37.50° N, 76.88° W	4 - 232	31 - 33
56° 30' N, 5° 22'W	0.1 to 0.3	0 - 25
56° 27' N, 5° 26' W	10 to 30	28 - 33
48° 45' N, 4° 0' W	10 to 30	25 - 33
48° 43' 3° 59' W	0 - 2	5 - 33
42° 35' N, 8° 46' E	20 - 200	35 - 37
40° 42' N, 13° 57' E	0.5 - 6	38
40° 42' N, 13° 57' E	0.5 - 6	35 - 37
45° 32' N, 13° 35' E	3 - 25	42
40° 44' N, 13° 56' E	< 31	38
40° 42' N, 13° 57' E	< 60	38
40° 45' N, 13° 57' E	6 - 10	36
40° 42' N, 13° 57' E	1.5	37
40° 28' N, 14° 53' E	0 to 2	17
40° 28' N, 14° 56' E	0 to 2	24 - 37
40° 39' N, 14° 45' E	12	12 - 20
40° 43' N, 14° 51' E	28	12 - 20
40° 31' N, 14° 54' E	1.8 - 9	38
45° 3' N, 13° 41' E	1 - 2	35
45° 32' N, 13° 35' E	0.5 - 6	38
45° 32' N, 13° 36' E	21 - 22	32 - 36
45° 33' N, 13° 35' E	18 to 20	36
45° 32' N, 13° 35' E	4	2 - 35
43 ° N, 5° E	1.5	37
32.94° N, 137.62° E	70 - 150	35
66° 0.8' S, 67° 58.6' E	300 to 600	35
46° 51' N, 17° 53' E	0.1	2

Coexisting Species

Apart from the three co-existing mysid species examined in detail in the previous chapter, three additional Tasmanian species, *Tasmanomysis oculata*, *Tenagomysis australis*, and *Australomysis acuta*, were included in the present study. Fenton (1992) reported that these species co-occur, but are not as common as the three species analyzed in the previous chapter.

Mysid species from the Republic of South Africa were kindly provided by Professor Tris Wooldridge of the Department of Zoology, University of Port Elizabeth. The four coexisting species, *Gastrosaccus brevifissura*, *G. psammodytes*, *Rhopalophthalmus terranatalis*, and *Mesopodopsis wooldridgei*, were collected from the Sundays River Estuary.

The three coexisting species, *Nipponomysis lingvura*, *Anisomysis ijimai*, and *Siriella longipes* from off Banda Beach, Tateyama Prefecture, Central Japan were kindly provided by Mr. Kuoki Fukuoka through the request of Professor Masaaki Murano. Both colleagues are from Tokyo University of Fisheries, Japan.

The two coexisting species from the northwest Philippines, *Gastrosaccus bengalensis* and *Siriella anomala* were gifts from Dr. Liana T. McManus during my visit to the Bolinao Marine Laboratory of the University of the Philippines' Marine Science Institute.

The seven species which occupy the eastern neritic region of North America, northeast of Central America (Western Atlantic), and Puerto Rico, namely: *Mysis mixta*, *Mysis stenolepis*, *Mysidopsis bigelowi*, *Anchialina typica*, *Erythrops erythrophthalma*, *Neomysis americana*, and *Bowmaniella brasiliensis*, were from the collection of the Department of Invertebrate Zoology (Crustacea), United States National Museum of Natural History, Smithsonian Institution. These specimens were promptly sent by the Department's Curator Emeritus, Dr. Thomas E. Bowman. Dr. Sture Hansson of the Department of Systematics and Ecology, University of Stockholm, Sweden also generously sent samples of *Mysis mixta* from the Northern Baltic Proper.

The rest of the coexisting species examined in the present study are from the

collection of Dr. Gwen E. Fenton of the Zoology Department, University of Tasmania. These species were collected from the English Channel, the coastal waters of Argyll, Scotland, and the Tyrrhenian and Adriatic Seas.

Single Species

Some of the species analyzed were without their sympatric species, thus they were regarded as single species. These mysids were examined mainly to increase the number of species being compared. They were again generously provided by Dr. Gwen Fenton of the Zoology Department, University of Tasmania. These include the marine cave species *Hemimysis speluncula* from the Gulf of Marseille, France; *Gastrosaccus indicus* from False Bay West, South Australia; *Antarctomysis maxima* from the deep waters off Mawson, Antarctica; and the freshwater species *Limnomysis benedeni* from Lake Balaton, Hungary.

Preparation of Specimens and Examination of Foregut Features

The removal of the foregut, and the subsequent dissection and histological processing are as described in chapter 8. Analysis of foregut features was performed using scanning electron microscopy. Some of the species which showed almost identical foregut features were not photographed, but were recorded on a videotape using a VCR attached to the scanning electron microscope. A copy of the videotape is deposited in the Zoology Department, University of Tasmania.

Habitat Association and Diet

Information on the habitat association and diet of all mysid species examined was obtained from published and unpublished references. However, in the case of the three additional Tasmanian species, the stomachs of 15 individuals of each of these species were dissected and the contents enumerated. The diet of some of the species, particularly those from the Philippine coral reef, neritic waters of the eastern North

America, Tyrrhenian Sea, Adriatic Sea, and some of the single species, is not well established. Stomach contents analysis of these specimens was limited to only 1-3 individuals of each species.

Treatment of Observations

Phylogenetic Analysis

Phylogenetic Analysis Using Parsimony (PAUP version 3.1.1, Swofford 1993) was used to estimate the topology of the hypothetical phylogenetic tree based on foregut morphology. The method essentially uses the Hennigian approach of most parsimonious characters examined in all taxonomic units in the tree generation. The PAUP analysis involves constructing the most parsimonious tree by simple "stepwise addition" heuristic search. Three taxa are chosen for the initial tree. One of the unplaced taxa is then chosen for the next addition. Each of the three trees that would result from joining the unplaced taxon to the tree along one of its three branches is evaluated and the optimal one is saved for the next round. In the next round five branches exist from the previous round and the process is repeated until all taxa are added to the tree. The algorithm then attempts to further optimize the tree by rearranging, a technique known as "branch swapping" (Swofford 1991).

Estimation of the true tree was completed by the resampling method of bootstrapping (Felsenstein 1985). This method is a form of statistical test which estimates confidence limits of internal branches in phylogenetic analyses. Characters in a matrix of taxa x can be sampled with replacement (bootstrapped) to create many new matrices of the same size as the original, each of which can be analyzed to find the best-fit tree (*e.g.* the shortest tree in the case of parsimonious analysis) (Hillis and Bull 1993). A caveat of this method, however, is that it provides us with a confidence interval within which is contained not the true phylogeny, but the phylogeny that would be estimated on repeated sampling of many characters from the underlying pool of characters (Felsenstein 1985). Although many studies treat bootstrap results as statements about the probability that a particular clade is a real historical group, the

method's estimates should provide an indication only of the degree of support of a particular technique for a particular clade (Hillis and Bull 1993). In condition of equal rates of change, proportions >70% usually correspond to a probability of ≥ 95% that the corresponding clade is real (Felsenstein and Kishino 1993). Reliance on the value of P depends whether a large P value over- or under-estimates the probability that the group is correct, *i.e.* whether the data are highly informative or not (Felsenstein and Kishino 1993).

Based on fossil statoliths, Ariani *et al.* (1992) noted that the oldest paleontological evidence of an inshore mysid belongs to the Sub-Family Rhopalophthalminae which dates back to the Carboniferous period (300-400 Mya). Assuming that this group is the most ancient, the foregut features of the extant representative *Rhophalophthalmus terranatalis* should still retain some of these ancestral characters. In the present analysis, this species was regarded as the taxon where character polarization was directed, *i.e.* foregut features in this reference species were treated as ancestral states.

Results

A total of 4 sub-families, 27 genera and 48 species in the Family Mysidae were surveyed in the present study. Table 9.2 below shows the published taxonomy of these species.

Table 9.2 Taxonomic classification of the different mysid species examined for foregut phylogenetic relationships (Marshall and Williams 1975). Other orders within the Division Peracarida are shown. Higher taxa belonging to the Sub-order Mysida follows the classificatory scheme of Mauchline (1980).

PHYLUM ARTHROPODA
CLASS CRUSTACEA
SUB-CLASS MALACOSTRACA
SERIES EUMALACOSTRACA
DIVISION PERACARIDA
  ORDER THERMOSBAENACEA
  ORDER SPELAEOGRIPHACEA
  ORDER **MYSIDACEA**
  ORDER CUMACEA
  ORDER TANAIDACEA

ORDER AMPHIPODA
ORDER ISOPODA
SUB-ORDER **MYSIDA**
FAMILY MYSIDAE
SUB-FAMILY SIRIELLINAE
GENUS *Siriella* Dana 1850
S. armata (M.-Edwards 1837)
S. anomala Hansen 1910
S. clausii G.O. Sars 1877
S. jaltensis gracilipes Czerniawsky 1868 ?
S. longipes Nakazawa 1910
SUB-FAMILY RHOPALOPHTHALMINAE
GENUS *Rhopalophthalmus* Illig 1906
R. terranatalis O. Tattersall 1957
SUB-FAMILY GASTROSACCINAE
GENUS *Anchialina* Norman and Scott 1906
A. typica (Krøyer 1861)
GENUS *Bowmaniella* Bacescu 1968
B. brasiliensis Bacescu 1968
GENUS *Gastrosaccus* Norman 1968
G. bengalensis Hansen 1910
G. brevifissura O. Tattersall 1952
G. indicus Hansen 1910
G. psammodytes O. Tattersall 1958
G. sanctus (van Beneden 1861)
GENUS *Haplostylus* Bacescu 1973
H. bacescui Hatzakis 1977
H. normani (tattersalli)
SUB-FAMILY MYSINAE
Tribe Erythropini
GENUS *Erythrops* G.O. Sars 1869
E. erythrophthalma
Tribe Leptomysini
GENUS *Australomysis* W. Tattersall 1927
A. acuta W. Tattersall 1907
GENUS *Leptomysis* G.O. Sars 1869
L. bürgii Bacescu 1966
L. gracilis (G.O. Sars 1864)
L. lingvura adriatica Wittmann?
L. lingvura marioni Gourret?
L. posidoniae Wittmann ?
GENUS *Mysidopsis* G.O. Sars 1864
M. gibbosa G.O. Sars 1864
M. bigelowi W. Tattersall 1927
GENUS *Pyroleptomysis* Wittmann 1985
P. rubra Wittmann 1985
GENUS *Tenagomysis* Thomson 1900
T. australis Fenton 1991
T. tasmaniae Fenton 1991
Tribe Mysini
GENUS *Acanthomysis* Czerniawsky 1882
A. longicornis (M.-Edwards, 1837)
GENUS *Anisomysis* Hansen 1910
A. ijimai (Nakazawa 1910)
A. mixta australis (Zimmer 1918)
GENUS *Antarctomysis* Coutière 1906
A. maxima (Hansen) Holt and Tattersall 1906
GENUS *Hemimysis* G.O. Sars 1869
H. lamornae mediterranea (Couch 1856)?
H. speluncula Ledoyer 1963

GENUS *Limnomysis* Czerniawsky 1882
L. benedeni Czerniawsky 1882
GENUS *Mesopodopsis* Czerniawsky 1882
M. slabberi van Beneden 1861
M. wooldridgei Wittmann 1992
GENUS *Mysis* Latreille 1803
M. mixta Lilljeborg 1852
M. stenolepis S.I. Smith 1873
GENUS *Neomysis* Czerniawsky 1882
N. integer Leach 1814
N. americana (S.I. Smith 1874)
GENUS *Nipponomysis* Murano 1986
N. lingvura Murano 1986
GENUS *Paramesopodopsis* Fenton 1985
P. rufa Fenton 1985
GENUS *Paramysis* Czerniawsky 1882
P. arenosa G.O. Sars 1877
P. nouveli Labat 1953
GENUS *Praunus* Leach 1814
P. flexuosus (Müller 1776)
P. neglectus (G.O. Sars 1869)
GENUS *Schistomysis* Norman 1892
S. assimilis (G.O. Sars 1977)
GENUS *Tasmanomysis* Fenton 1985
T. oculata Fenton 1985

Table 9.3 Spine types undescribed in the three Tasmanian mysid species (Table 8.4), but found in the additional species analyzed

Type	Location	Description
4.1	laterale	broad based, thin and long, with fine spinules
8.1	laterale	pronged, with broad-based sharp spinules
8.2	laterale	unpronged, with broad-based sharp spinules
19	laterale	pronged, broad-based, robust or tooth-like
20	anteromedianum	unpronged, round-based, with fine spinules

Foregut Features

The foreguts of the additional 45 species are described and compared with reference to the foregut features of the three coexisting Tasmanian mysid species

which were regarded as the "standard" species.

Co-occurring Mysids from Sundays River Beach, Port Elizabeth, Republic of South Africa

The gross shape of the foregut stomach of *Rhopalophthalmus terranatalis* is spheroidal. Like that in *P. rufa*, the anterior cardiac chamber is swollen. All the ridges and regions in the cardiac and pyloric chambers are present. The laterale differs from those in the standard foreguts in terms of the types of spines present on its anterior edge. The anterior laterale spines (ALS) comprise two isolated type 8.1 spines (Fig. 9.2A,E; Table 9.3). Types 2 and 4 spines arm the anterior laterale's middle edge and the posterior dorsal surface of the laterale (Fig. 9.2E). On the medial portion of the anterior laterale's edge, robust type 19 spines curve and point dorsally (Fig. 9.2E; Table 9.3). Dense type 5 spine clusters are also present on the posterior dorsal portion of the laterale (Fig. 9.2F). The postero-lateral spines (PLS) are absent, but a posterolateral tooth (PLT) is present (Fig. 9.2A,E). The dorsal surface of the laterale bears few type 3 spines (Fig. 9.2F). The edge above the primary filter is lined with types 5 and 6 spines. The anteromedianum is covered on both sides with short and soft spinules, and the row of type 20 spines (Table 9.3) project from its pinnacle. The posterior region of the anteromedianum becomes flatter and on its dorsal surface very short and stout spines project. The spines comprising the primary filter are similar to those found in the typical primary filter. In *R. terranatalis*, three isolated and robust teeth comprise the cardiac dorsolateral teeth (CDLT) (Fig. 9.2A,F,B). Each tooth is similar to that found in *P. rufa* CDLT; it is saw-like and with a pointed tip (Fig. 9.2B). The cardiac ventrolateral teeth (CVLT) are unclustered, and consist of four isolated teeth with denticulations on the ventral edge (Fig. 9.2C,G). Two densely barbed "horns" flank the anterior portion of the cardiac dorsal piece (CDP). The rest of the CDP features are similar to those in the standard foreguts.

Gastrosaccus brevifissura and *G. psammodytes* are described together because they show very similar foregut features. Scanning electron micrographs of the foreguts of these species are shown in Figure 9.3. The foreguts of both species are

Figure 9.2 Foregut features of *Rhopalophthalmus terranatalis*. A. anterodorsal view showing laterale (l) and associated spines (als, type 2 spines, plt), am, pf, cdlt, cvlt, posterior superolaterale (psl), pamr. B. left cdlt. C. left cvlt. D. cdp and the single horn (h). E. close-up of left laterale (l) and associated spines (als, plt, types 2, 4, 19), inset - type 19 spines. F. mediolateral view of inner surface of laterale (l) showing type 6 spines above the primary filter (pf), types 2, 3, 5 spines, cdlt, cvlt. G. right cdlt. H. close-up of the anterior single horn (h) of the cdp. Scale bar: A, D-F = 0.1 mm; B, C, E and inset, G, H = 10 μm.

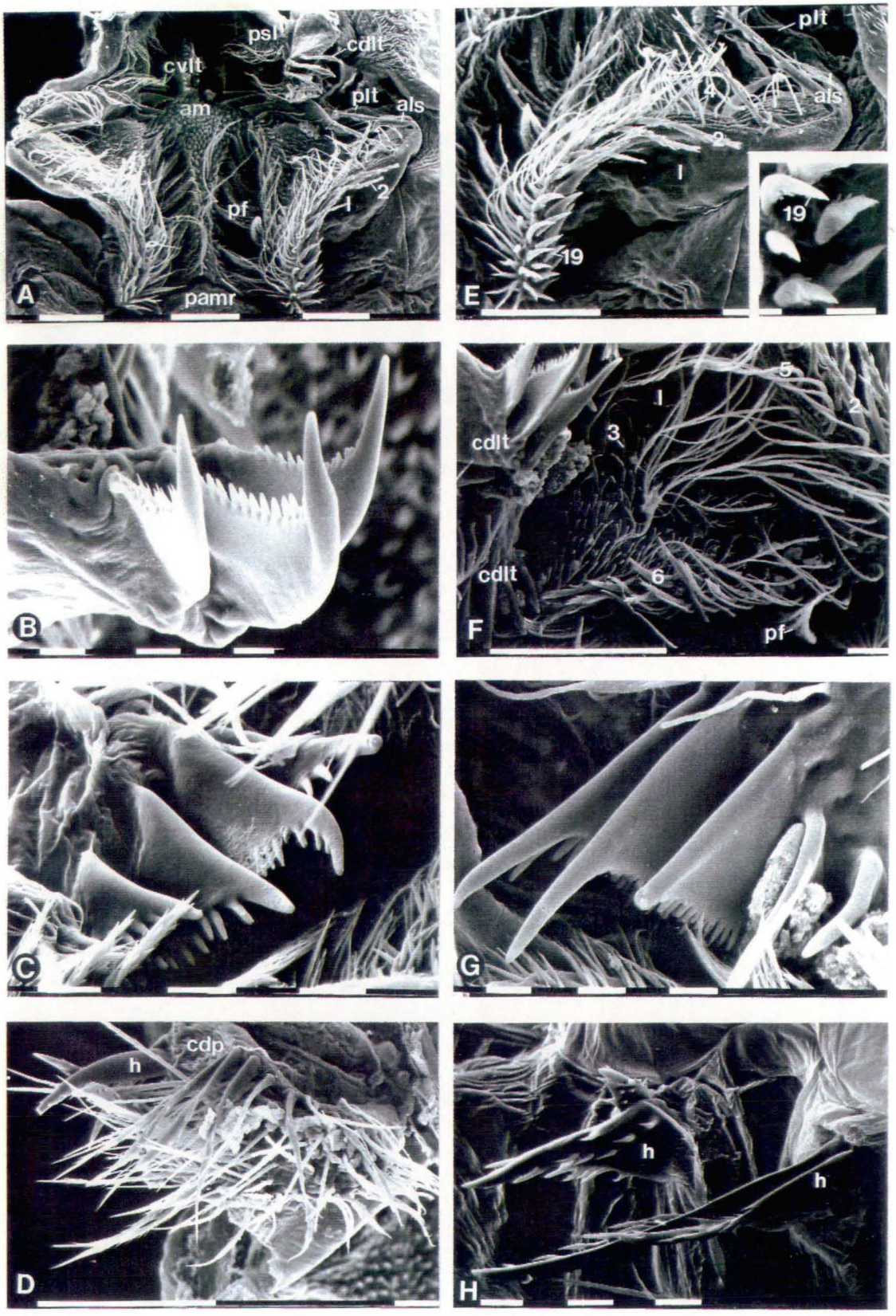
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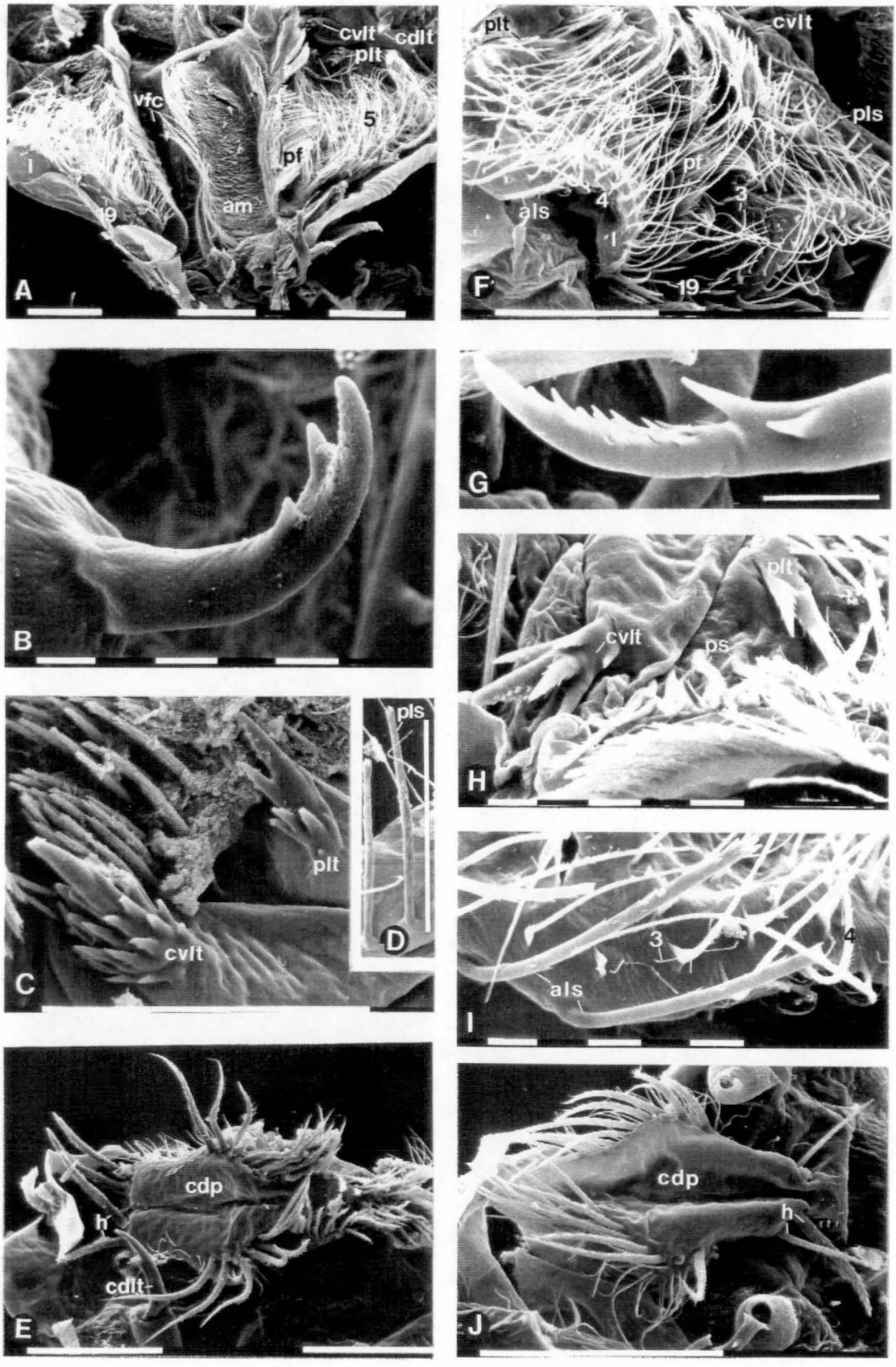
Figure 9.3 Foregut features of *Gastrosaccus psammodytes* (A-E), and *G. brevifissura*; (F-J). A. anterodorsal view showing the laterale (l) and spines (types 5, 19), am, cdlt, cvlt, pf, plt, vfc. B. left cdlt. C. right cvlt, and plt. D. pls. E. cdlt, cdp and its double anterior horns (h). F. anterodorsal (slightly tilted to the right) view, showing laterale (l) and associated spines (als, types 3, 4, 19), cvlt; pf, pls, plt. G. left cdlt. H. left cvlt, plt, and spines on the the posterior laterale (ps). I. als, and types 3, 4 spines. J. cdp, and its prominent anterior horns (h) and companion spine (cs). Scale bar: A, C-F, J = 0.1 mm; B, G, H, I = 10 μm.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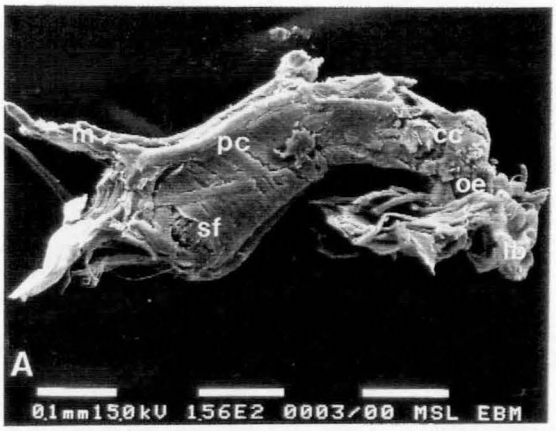
spheroidal. All cuticular ridges in both the cardiac and pyloric chambers, and the various circulation canals are present. Their lateralia possess long and curved spines with distribution different from those in the standard laterale. The ALS, for instance, are not clustered, and comprise 2 to 3 isolated type 8.1 spines (Fig. 9.3I; Table 9.3). The anterior edge of the laterale is mainly composed of type 4.1 spines (Table 9.3) which are also present on the dorsal surface of the laterale (Fig. 9.3I). Very few type 3 spines are found on the dorsal surface of the laterale. Type 19 spines project from the medial edge of the anterior laterale (Fig. 9.3A,F). The posterior surface of the laterale bears type 6 spines which also form a row just above the primary filter spines (Fig. 9.3H). The PLS is composed of 6 type 8.1 spines (Fig. 9.3D). Just behind the most posterior PLS projects the postero-lateral tooth (Fig. 9.3C,F,H). This structure is homologous to the PLT of *R. terranatalis*. The anteromedianum of both species is similar to that found in *T. tasmaniae*, in that it possesses short spines on both sides and a row of type 20 spines on its pinnacle (Fig. 9.3A,F). Its most posterior portion does not have a tongue-like structure projecting towards the dorsal channel of the pyloric region. The CDLT are pointed and curved with two large and a few small broad-based denticles on the distal portion of the shaft (Fig. 9.3B,G). The CVLT are clustered, and appear very similar to the PLT, except they comprise more component teeth (Fig. 9.3A,C,F,H). The cardiac dorsal piece in these species is distinct because apart from having the "horns" (four in *G. psammodytes* (Fig. 9.3E), and one in *G. brevifissura* (Fig. 9.3J), the central surface does not bear spines. Stout spines are found projecting on both lateral margins of the piece. Six of these spines are the type 13 found in the three "standard" species, and the rest are types 3, 5, and 17 spines.

The anterior cardiac chamber in *Mesopodopsis wooldridgei* is tubular which differs entirely from the spheroidal gross form of the standard mysid foregut (Fig. 9.4A). The structures in the pyloric chamber are similar to the standard foregut. The change in gross form of the anterior cardiac chamber is associated with dramatic changes in the internal structures. Elaborate spination is not found on the surfaces of the cardiac chamber ridges (Fig. 9.4B). The laterale stretches through the entire length

Figure 9.4 Foregut features of *Mesopodopsis slabberi* (A and B) and *M. wooldridgei* (C-E). A. lateral view showing labrum (lb), oe, cc, pyloric chamber (pc), sf, dorsal muscle (m). B. laterale (l) and spines (als), am, and vfc. C. anterodorsal view showing laterale (l) and spines (as), primary filter (pf) ridges, and posterior portion of the anteromedianum (am). D. close-up of the lateral view of laterale and associated spines (as), and a portion of the primary filter (pf) ridge. E. close-up of pf, anterodorsal view of both laterale (l) and spines (as). Scale bar: A - D = 0.1; E = 10 μm.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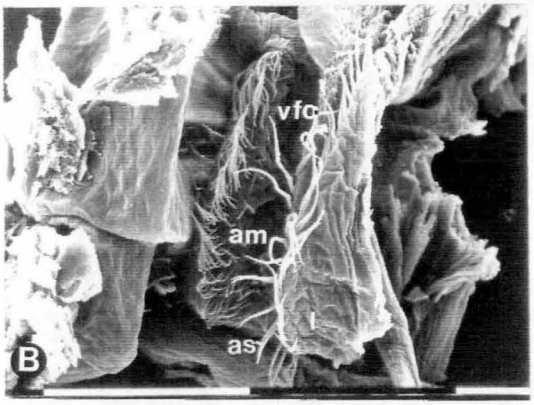
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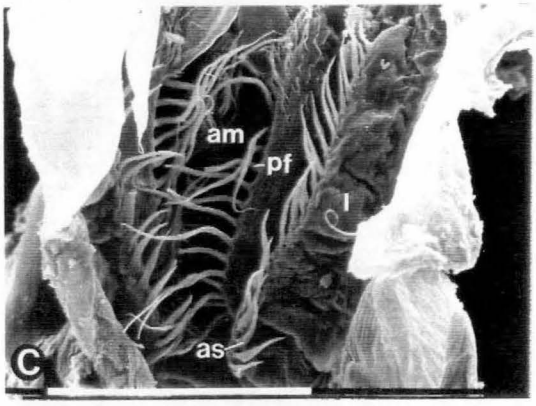
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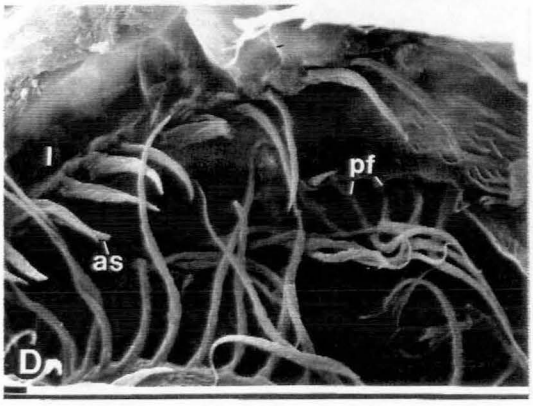
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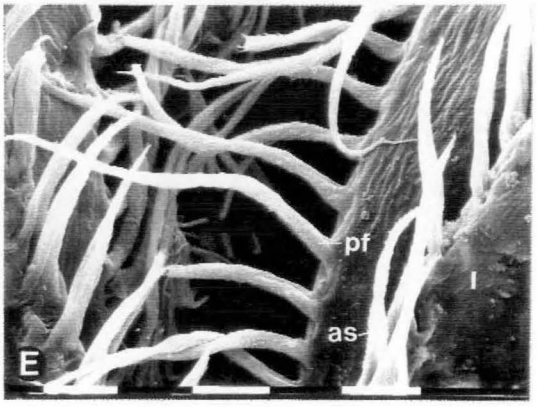
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of the cardiac chamber, and bears a row of widely spaced spines on the medial edge (Fig. 9.4D,E). These spines project horizontally to the cavity of the cardiac chamber, and are stout at the base and taper towards the tip. Short and thin spinules project from the underside of the distal portions. Spines are absent on both the anterior and ventral surfaces of the laterale. Almost similar in length to the laterale, and stretching underneath the laterale is the primary filter ridge (Fig. 9.4D,E). The orientation of the spines of the laterale and this ridge appears to form a two storeyed "primary sieve" in the cardiac chamber (Fig. 9.4D). These spines which are longer than those in the laterale intermesh with those spines on the opposite primary filter ridge. The most posterior dorsal surface of the primary filter ridge bears soft and short spines. The anteromedianum is similar in form to those found in the standard foregut, but only short and soft spines project on the pinnacle (Fig. 9.4B,C). The CVLT, CDLT, and CDP are absent.

Co-occurring mysids from off Banda Beach, Tateyama Prefecture, Central Japan

Like that in *Anisomysis mixta australis*, the foregut shape of *A. ijimai* is spheroidal and shows no elaborate foldings. This species only differs from *A. mixta australis* by the types of spines on the laterale. Apart from this, the different armatures found in the cardiac stomach (Fig. 9.5F,G) are identical. The ALS of this species is composed of robust spines which are pronged at their tips (Fig. 9.5G). These spines, however, are different from those of *A. mixta australis* for their shafts bear robust spinulations. The PLS are much reduced type 11 spines, and lack the type 9 spines (Fig. 9.5G). The spines on the surface, edge, and posterior region of the laterale, the CDLT (Fig. 9.5H) and CVLT (Fig. 9.5H,I), the spines on the anteromedianum, and the CDP (Fig. 9.5J) are very similar to those found in *A. mixta australis*.

Nipponomysis lingvura shows the standard spheroidal foregut shape. The elaborate spination on the laterale of the cardiac stomach, is very similar to that found in *T. tasmaniae* (Fig. 9.6A,B). The ALS consist of clustered type 8.1 spines (Fig.

9.6A,B; Table 9.3), and the edge of the anterior laterale is composed of all spine types (Fig. 9.6B). The dorsal surface of the laterale is densely covered with types 3, 5 and 7 spines. The PLS are broad-based with sharp unpronged tips and fine spinulations on the shafts. The anteromedianum also bears on its pinnacle posteriorly curved type 20 spines (Fig. 9.6A). The CDLT is composed of two sharply denticulated teeth (Fig. 9.6C); the CVLT is unclustered and is composed of 5 component teeth (Fig. 9.6D). The teeth increase in size posteriorly, and as found in the other described CVLTs, the denticulations are on the ventral aspect of each tooth. The CDP is similar to that of *T. tasmaniae* (Fig. 9.6E).

The gross shape of the foregut of *Siriella longipes* is also spheroidal, but a median dorsoventral infolding is present on the anterodorsal roof of the cardiac region. The ALS is composed of widely gapped isolated type 8.1 spines (Fig. 9.7A). The tips of these spines point towards the medial space of the cardiac chamber. No other spine types are found on the edge of the laterale except the type 21 spines which project between two successive ALS spines. The medial edge of the laterale bears a cluster of similar ALS spines with their pronged-tips pointing dorsally. The rest of the dorsal surface of the laterale bears very few type 3 spines. The anteromedianum bears no type 20 spines on its pinnacle, but short spines are present. Aside from being clustered in appearance, the CVLT (Fig. 9.7E) are smooth as in *P. rufa*, but the most distal portions of each tooth are curved posteriorly. The single pair of hook-like CDLT flanks the CDP (Fig. 9.7C). Each tooth bears few small and blunt denticles on its curvature. The CDP is simple and bears types 13, 15, and 17 spines concentrated on the lateral margins of the piece (Fig. 9.7C). Few long thin spines are found on the posterior central area of the CDP.

Co-occurring Mysids from the Neritic Waters of North America

All seven species possess spheroidal foreguts, and the basic features are similar to those in the standard foregut. Descriptions are focused on the differences in type, disposition, distribution and density of the spines and teeth in the cardiac chamber. With the exception of *M. bigelowi* which lacks the structure, the rest of the

Figure 9.5 Foregut features of *Mysidopsis bigelowi* (A-E) and *Anisomysis ijimai* (F-J). A. anterodorsal view showing laterale (l) and associated teeth (alt) and spines (als), am, pf, cvlt. B. close-up of left laterale(l) and associated teeth (alt) and spines (als, types 3, 19). C. right cdlt. D. right cvlt. E. cdp showing marginal teeth (mt) and medial spines (ms). F. anterodorsal view showing laterale (l) and associated spines (als, type 19, pls), am, lcc, pf, cdlt; cvlt. G. close-up of lcc, and left laterale and associated spines (als, types 3, 4, pls). H. left cdlt and cvlt. I. left cvlt. J. cdp. Scale bar: A, B, F, G, J = 0.1 mm; C-E, H, I = 10 μm.

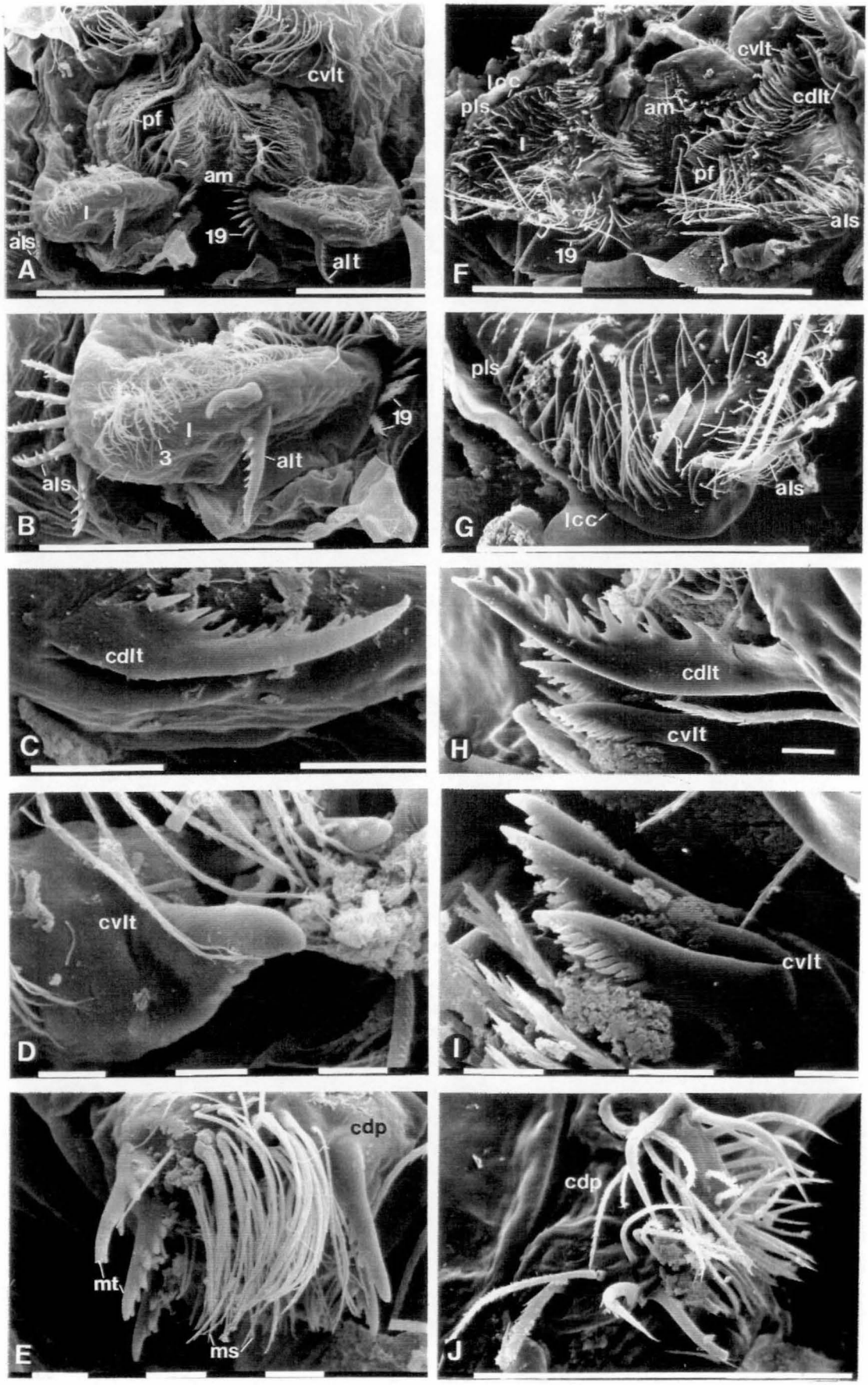
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Figure 9.6 Foregut features of *Nipponomysis lingvura* (A-E) and *Erythrops erythrophthalma* (F-J). A. anterodorsal view showing laterale (l) and associated spines (als, pls, type 1), am, vfc, lcc, pf, cdlt, cvlt, inferolaterale (il) of pyloric region. B. close-up of left laterale (l) and associated spines (als, types 1, 4, 5). C. cardio-pyloric junction showing cdlt, cvlt. D. right cvlt; E. cdp. F. anterodorsal view, showing laterale (l) and associated spines (als), am, pf, cdlt, cvlt, pamr, inferolaterale (il) of pyloric region. G. lcc, pls, and type 3 spines. H. right cdlt; I. right cvlt; J. cdp. Scale bar: A-E, F-H, J = 0.1 mm; D, I = 10 μm.

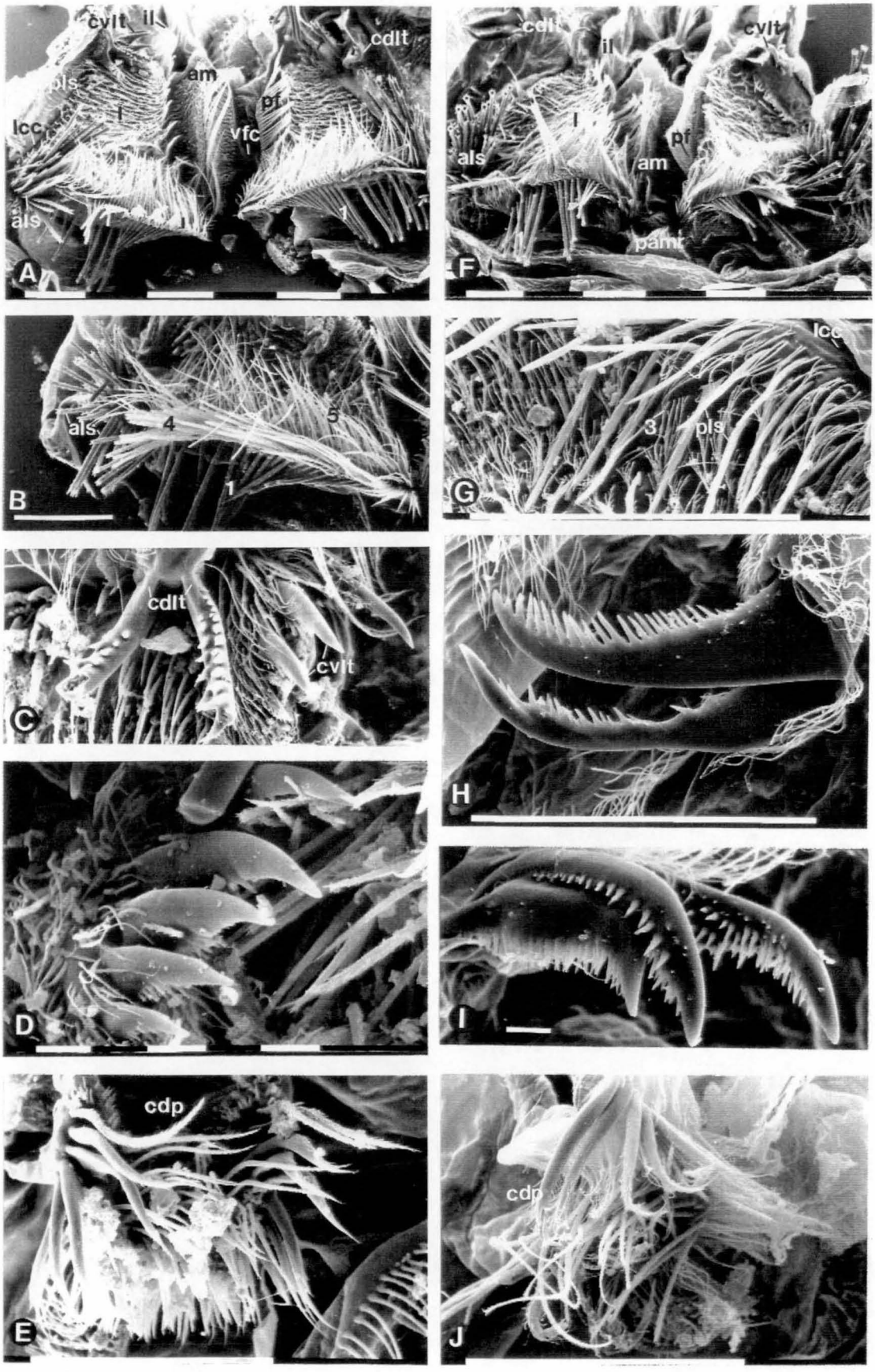
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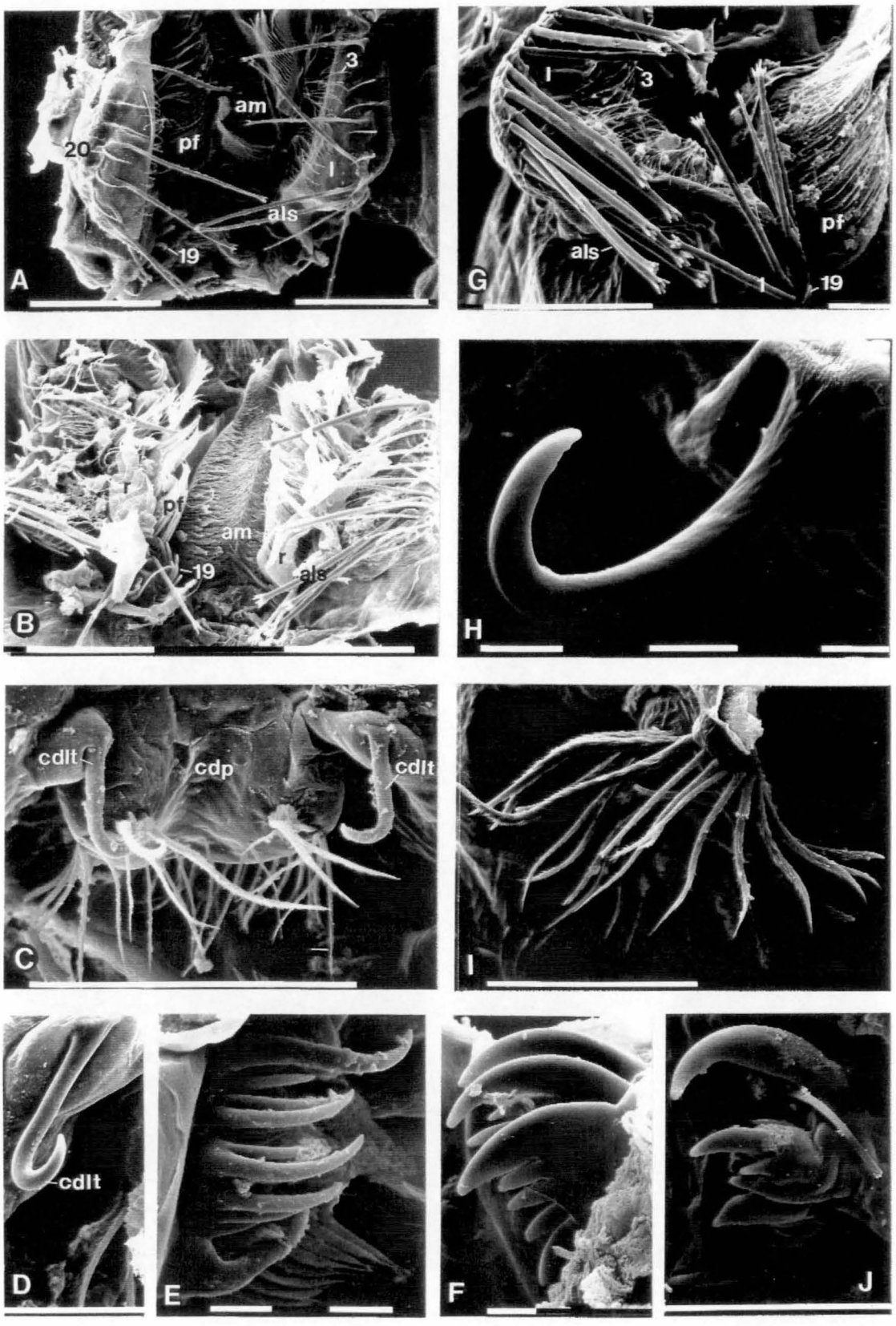
Figure 9.7 Foregut features of *Siriella longipes* (A, C, E), *S. anomala* (B, D, F), and *S. armata* (G - J). A. anterodorsal view showing the laterale (l) and associated spines (als, types 3, 19, 20), pf, am. C. left and right cdlt, and cdp. E. right cvlt. B. anterodorsal view showing als, pf, am, type19 spine, and crustacean remains (r). D. right cdlt. F. left cvlt. G. anterodorsal view of anterior laterale (l) showing als, types 1, 3, 19 spines, pf. H. left cdlt. I. lateral view of cdp. J. left cvlt. Scale bar: A-C, G, I = 0.1 mm; D = 40.3 μm; E = 10 μm; F,J = 60.7 μm.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six species possess an anteromedianum which bears a single row of type 20 spines on its pinnacle.

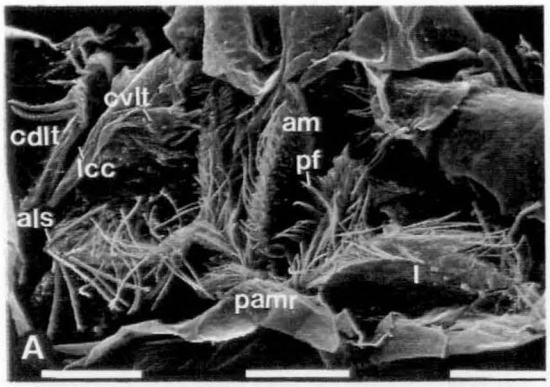
In *Anchialina typica*, only two rows of types 4 and 5 spines are present on the anterior edge of the laterale (Fig. 9.8F). The ALS comprises 3 to 5 unclustered type 8.2 spines (Fig. 9.8F; Table 9.3). The shafts of these spines are covered with dense broad based spinules. The anterior portion of the laterale's dorsal surface bears few type 3 spines, but the posterior portion bears a combination of types 3 and 5 spines (Fig. 9.8F). The posterior laterale tooth (PLT) and the less robust PLS (Fig. 9.8F,J) are present. The CDLT comprises two component teeth similar to those in *P. rufa* (Fig. 9.8G). Each tooth is flat, and sharp denticles arm the dorsal edge. The CVLT is clustered and consists of 8 to 9 apices, and each component tooth bears denticulations on its ventral aspect (Fig. 9.8H). The CDP is similar to those in *R. terranatalis* and the *Gastrosaccus* species, because it bears a pair of anterior horns, and the spines line the lateral margin (Fig. 9.8I).

The features of the cardiac region of *Bowmaniella brasiliensis* (Fig. 9.9D-F) are very similar to those in the *Gastrosaccus* and *Haplostylus* group already described. The presence of four pairs of horns on the anterior part of the CDP (Fig. 9.9F) is unique to this species.

In *Erythrops erythrophthalma*, all four rows of types 1, 3, 4 and 5 spines arm the anterior edge of laterale (Fig. 9.6F). The densely clustered ALS is composed of type 8 spines (Fig. 9.6F). The posterior surface of the anterior laterale bears both types 1 and 5 spines, but dense type 1 spines project from the laterale's dorsal surface. Finely spinulated, unpronged, and less robust spines form the PLS (Fig. 9.6G). The unclustered CDLT (Fig. 9.6H) is composed of 2 component teeth with denticulations on the dorsal aspect of the shaft. The clustered CVLT comprise three sharp apices, and the ventral aspect of the component teeth are heavily armed with sharp denticulations (Fig. 9.6I). The CDP is simple and comprises the component spines (Fig. 9.6J).

Mysidopsis bigelowi is the smallest of the seven North American species.

Figure 9.8 Foregut features of *Paramysis nouveli* (A-D) and *Anchialina typica* (E-J). A. antero-dorsal view showing laterale (l) and and associated spines, (als), am, cvlt, cdlt, pf, lcc, pamr. B. close-up of right laterale and associated spines (als, types 3, 4). C. right cdlt. D. right cvlt. E. anterodorsal view showing laterale (l) and associated spines and teeth (als, pls, plt, type 19, 4), pf, am, cvlt, cdlt. F. mediolateral view showing pf, left laterale and associated spines (als, pls, types 3, 4, 5, 6, 19) and tooth (plt). G. right cdlt. H. right cvlt. I. cdlt, cdp with single anterior horn (h), CDLT. J. pls, plt, type 3 spine. Scale bar: A, B, D-F, I = 0.1 mm; C, G, H, J = 10 μm.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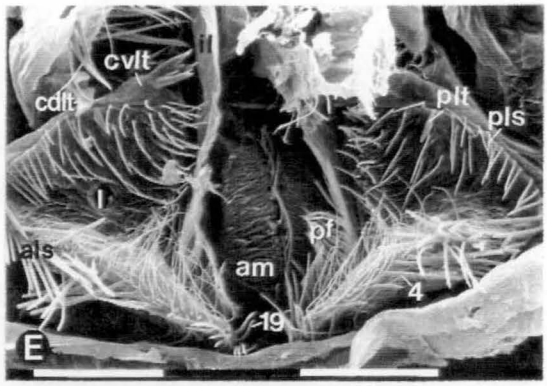
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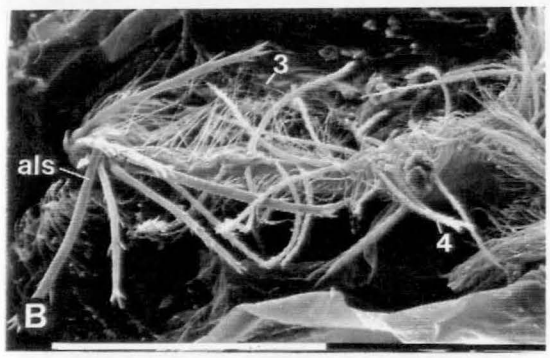
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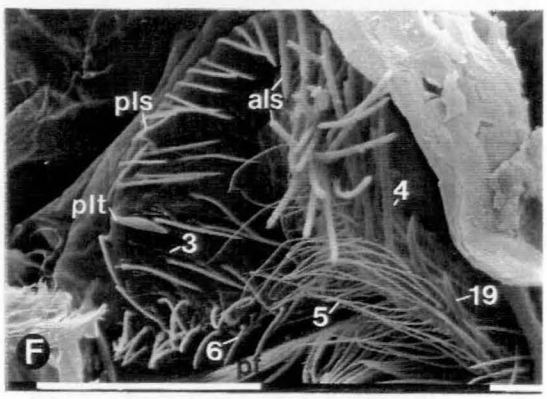
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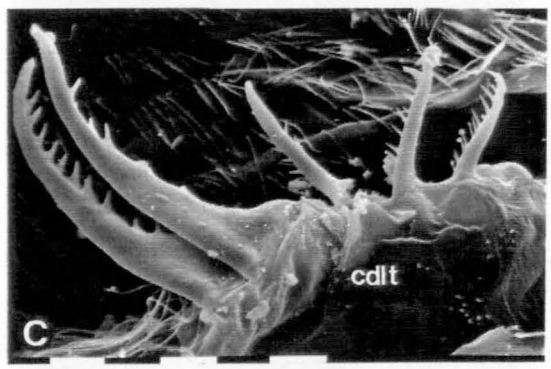
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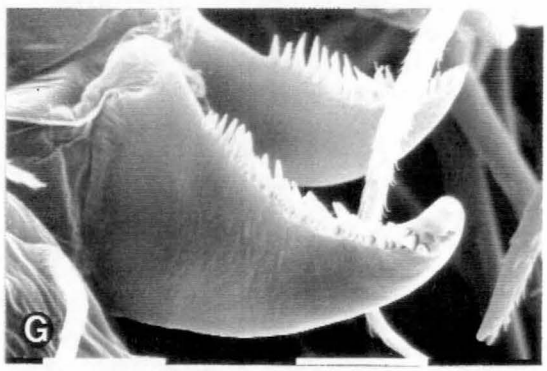
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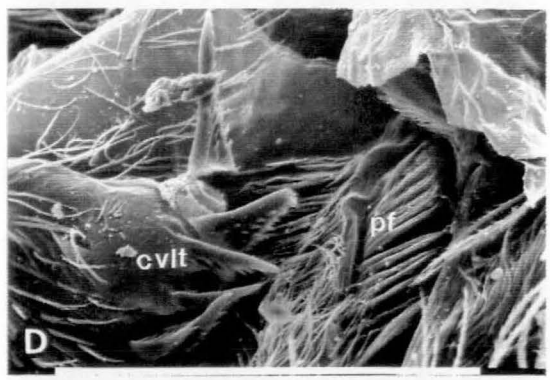
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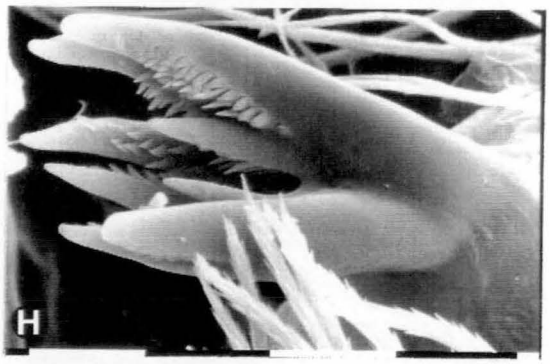
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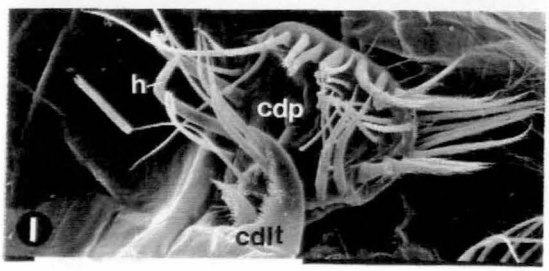
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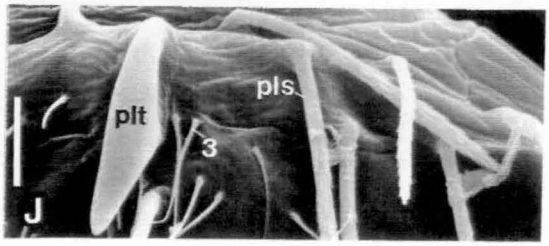
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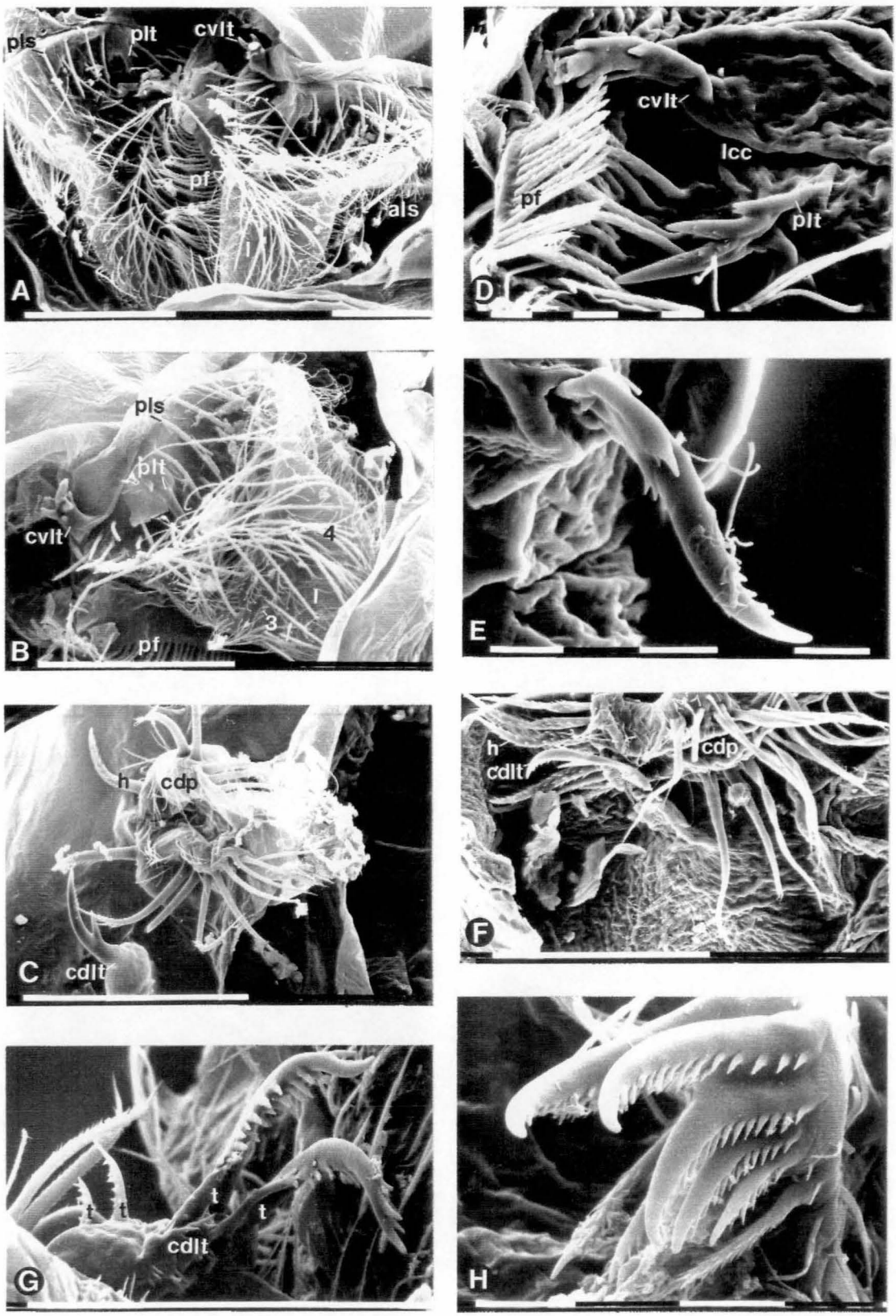
Figure 9.9 Foregut features of *Gastrosaccus bengalensis* (A-C), *Bowmaniella brasiliensis* (D-F), and *Hemimysis lamornae mediterranea* (G and H). A. anterodorsal view showing laterale (l) and associated spines (als, pls) and tooth (plt), pf, cvlt. B. mediolateral view of left laterale(l) showing pls, types 3 and 4 spines, plt, pf, cvlt, pf. C. cdlt, cdp and its pair of single horn (h). D. plt, cvlt, lcc, pf. E. right cdlt. F. cdlt, cdp with a pair of quadruple horns (h). G. left cdlt. H, left cvlt (individual tooth (t)). Scale bar: A-C, F, G = 0.1 mm; D, E, H = 10 μm.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Few of type 5 spines are found on the anterior edge of the laterale (Fig. 9.5A,B). In addition, two denticulated teeth project from the middle portion of the edge (Fig. 9.5A,B). The medial edge of the laterale bears robust and spinulated type 19 spines which point dorsally (Fig. 9.5A,B). The unclustered ALS is composed of five sharply denticulated teeth similar to those teeth found on the anterior edge of the laterale (Fig. 9.5B). The remainder of the laterale bears very few type 3 spines. The PLS is absent in this species. There is only one denticulated CDLT (Fig. 9.5C). The clustered CVLT bears two blunt apices, and the denticulations on the component teeth are also blunt (Fig. 9.5D). The CDP is unique in that it bears a patch of type 17 spines in the central area, and three pairs of denticulated teeth on the lateral margins (Fig. 9.5E). No horns are found on the anterior portion of the CDP.

The foregut features of *Mysis mixta* and *Mysis stenolepis* are similar to those in *T. tasmaniae*. All four types of spines form rows on the anterior edge of the laterale, and few clustered type 8.1 spines form the ALS (Fig. 9.10A,F). The dorsal surface of the remainder of the laterale is dominated by both types 3 and 5 spines. The PLS is composed of two to three rows of unpronged, and less robust spines (Fig. 9.10E,K). The two species only differ in the number of CDLT component teeth, in that *M. stenolepis* has 4 (Fig. 9.10B) while *M. mixta* has 5 (Fig. 9.10G). The clustered CVLTs of the two species are very similar and comprise several apices of component teeth with sharp denticulations on the ventral aspect (Fig. 9.10C,H). The CDP is simple and comprises all types of spines as in the standard foregut.

The projections on the cardiac chamber in the foregut of *Neomysis americana* are similar to those found in *T. tasmaniae* (Fig. 9.11A,E). The anterior edge of the laterale bears rows of all four types of spines (types 1, 3, 4, 5) and a few of the type 8.1 clustered ALS (Fig. 9.11A). Few type 3 spines are found on the remainder of the laterale. The few PLS are less robust than those found in *N. integer* (Fig. 9.11E). The CDLT has two component teeth (Fig. 9.11B), and the unclustered CVLT has three (Fig. 9.11C). The CVLT, however, are smaller and less denticulated than those in *N. integer*. The CDP (Fig. 9.11D) is simple and bears the same types of spines as in the standard foregut type.

Figure 9.10 Foregut features of *Mysis stenolepis* (A-E) and *M. mixta* (F-K). A. anterodorsal view showing laterale (l) and associated spines (als, type 1), am, pf, cdlt, cdp, vfc, psl, inferomedianum (im), il, lcc. B. right cdlt (individual tooth (t)). C. right cvlt. D. cdp. E. pls. F. anterodorsal view of left laterale (l) and associated spines (als, pls, types 1, 5), pf, am, cdlt, vfc. G. left cdlt (individual tooth (t)). H. pf, left cvlt. I. lateral view of left half of cdp. J. close-up of the spinules on the primary filter spines. K. pls. Scale bar: A = 1 mm; B-D, F-I = 0.1 mm; E = 32.6 μm; J = 7.4 μm; K = 22 μm.

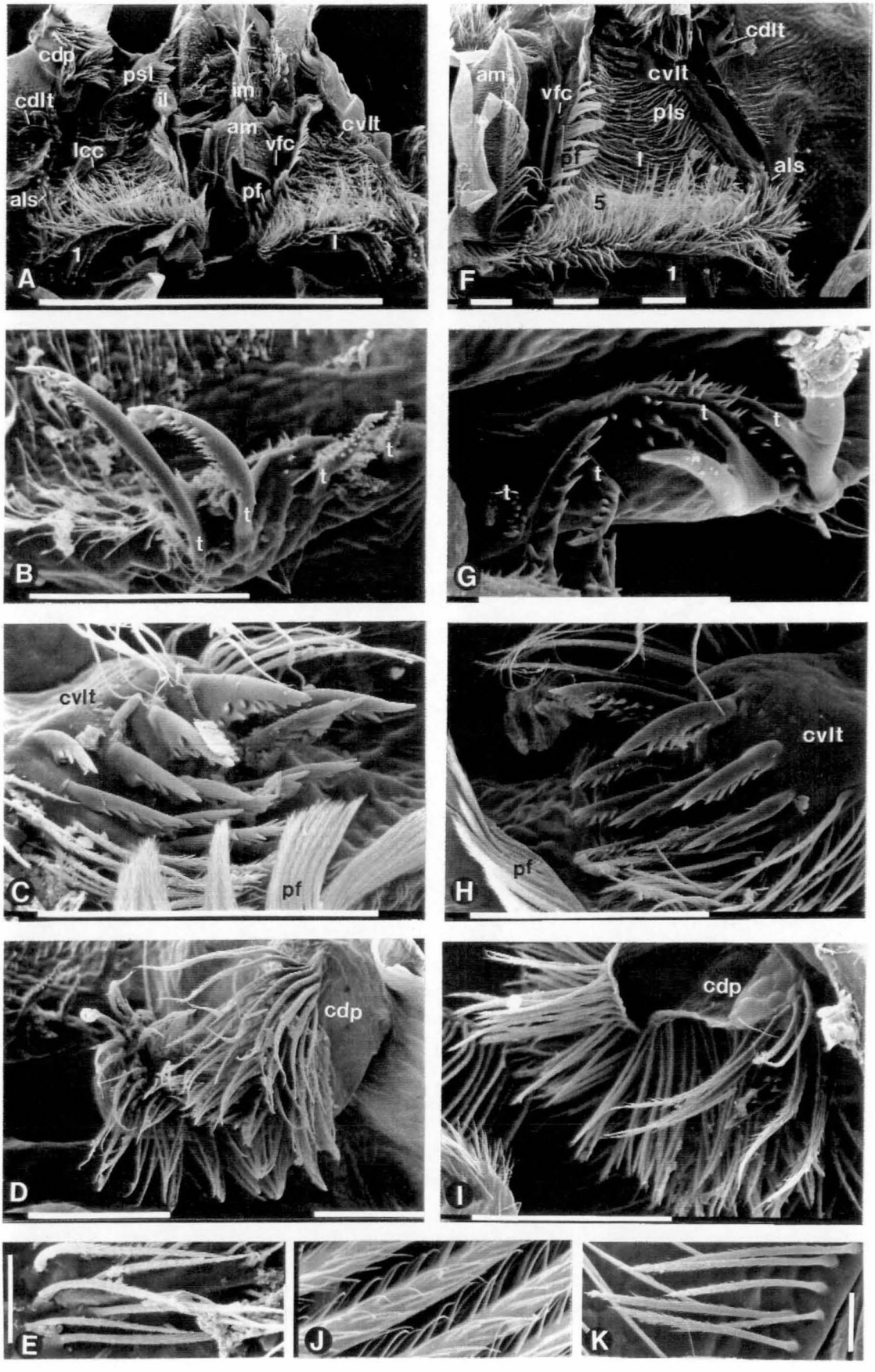
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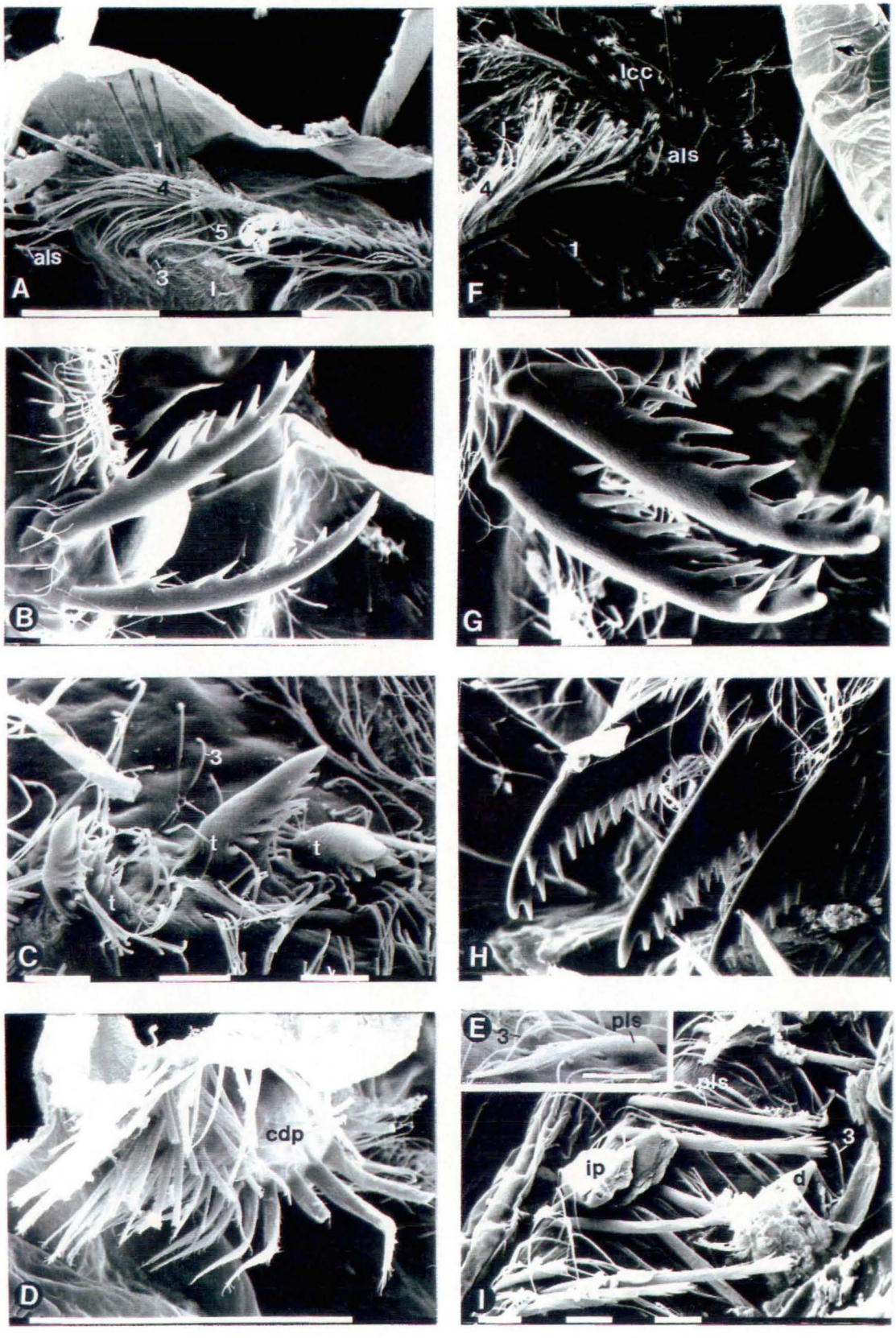
Figure 9.11 Foregut features of the *Neomysis* foregut type. A-E, *N. americana*; F-I, *N. integer*. A. close-up of dorsal view of left anterior laterale (l) and associated spines (als, types 1, 3, 4, 5). B. right cdlt. C. right cvlt (individual tooth (t)). D. cdp. E. pls and type 3 spines. F. close-up of lcc and left laterale (l) and associated spines (als, types 1, and 4). G. right cdlt. H. left cvlt. I. pls, type 3 spines, and stomach contents (diatom (d), inorganic particle (ip)). Scale bar: A, B, D, F, H = 0.1 mm; C, G, E, I = 10 μm.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Foregut Morphology of Two Co-occurring Mysids from Northwestern Philippines Coral Reef

The foregut features of *Gastrosaccus bengalensis* and *Siriella anomala* are very similar to those described previously for the same genera. Figures 9.9A,B show the armatures on the laterale of *G. bengalensis* foregut. The CDP of *G. bengalensis* (Fig. 9.9C) is similar to that of *G. brevifissura* in having a single anterior horn and stout spines on the margins. The foregut features in *S. anomala* are shown in Figure 9.7B,D,F.

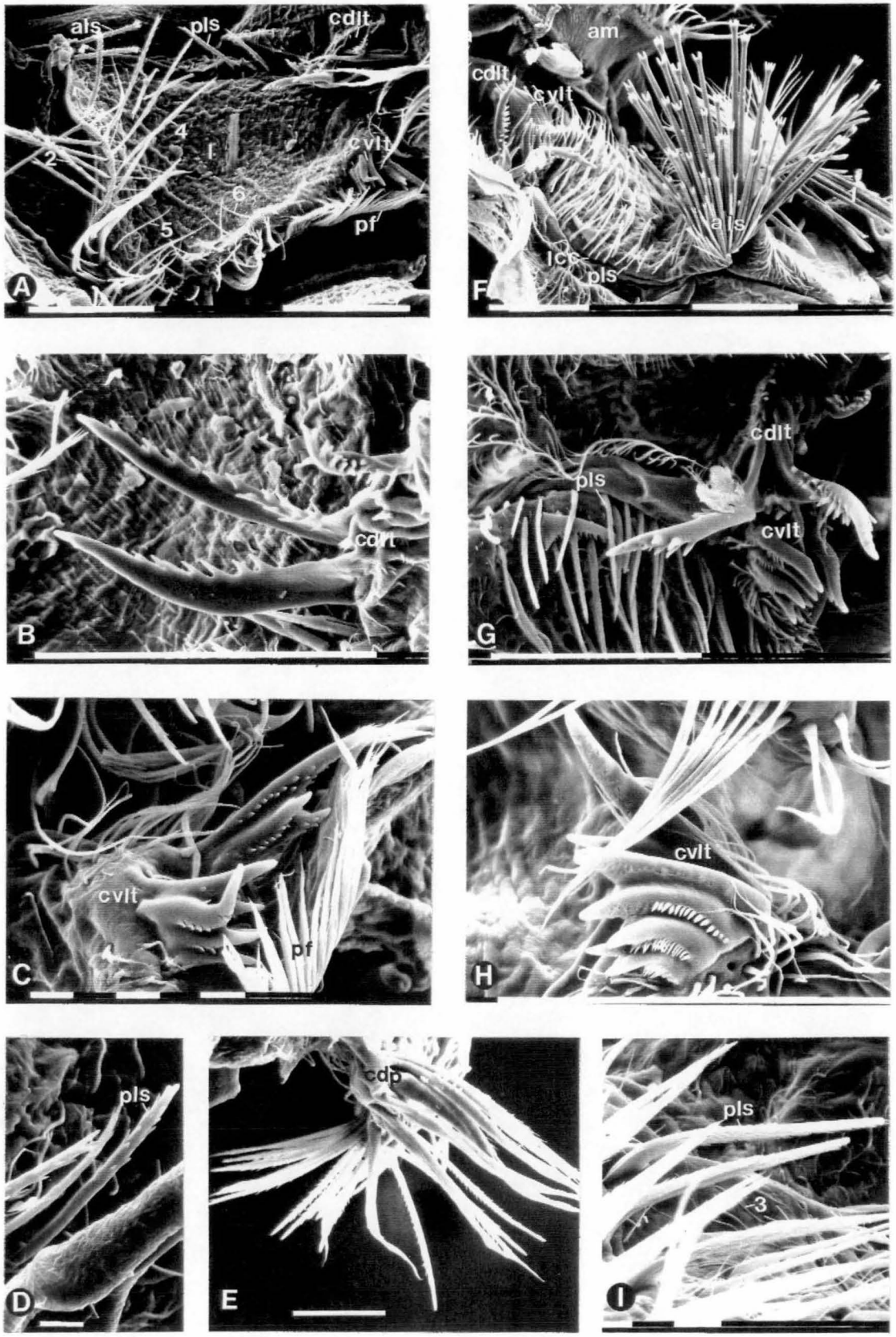
The Other Southeast Tasmanian Species

Australomysis acuta has very similar foregut features to those in *T. tasmaniae*. The features in *Tenagomysis australis* also closely resemble those in its congener, *T. tasmaniae* (Fig. 9.12 F-I). Its ALS is clustered (Fig. 9.12F), all spine types are present on the surfaces of the anterior laterale, three teeth comprise the CDLT (Fig. 9.12G), its CVLT is clustered and denticulated (Fig.9.12H), but the PLS (Fig. 9.12I) are less robust than those in *T. tasmaniae*. *Tasmanomysis oculata*, the largest of the southeast Tasmanian species examined, shows foregut features (Fig. 9.12A-E) similar to those of the three standard mysid foreguts. Few Types 2 and 4 spines form rows on the anterior edge of the laterale, and 2-3 unclustered spines form the ALS (Fig. 9.12A). Mainly type 3 spines are found on the dorsal surface of the laterale (Fig. 9.12 A,B). Its PLS comprise robust spines with broad based spinules (Fig. 9.12D). The anteromedianum bears a row of type 20 spines on the pinnacle. Three component teeth comprise the CDLT of *T. oculata* (Fig. 9.12B), and its CDLT is clustered and denticulated (Fig. 9.14C). Its CDP (Fig. 9.12E) is similar to that in the three standard mysid species.

Species from Off Argyll, Scotland and the English Channel

The foregut features of *Neomysis integer* (Fig. 9.11F-I) are similar to those in *T. tasmaniae* and in its congener, *N. americana*. All spine types are found on the anterior laterale, and its ALS are clustered (Fig. 9.11F), but fewer than those in *T.*

Figure 9.12 Foregut features of *Tasmanomysis oculata* (A-E), and *Tenagomysis australis* (F-I). A. mediolateral view of right laterale (l) and associated spines (als, pls, types, 2, 4, 5, 6), pf, cdlt, cvlt. B. right cdlt. C. pf, right cvlt. D. pls. E. cdp. F. dorsal view of the right laterale showing associated spines (als, pls, type1), am, cdlt, cvlt, lcc. G. close-up of right cdlt, cvlt, pls. H. left cdlt. I. pls and type 3 spines. Scale bar: A, B, F-H = 0.1 mm; C, D, I = 10 µm; E = 30.6 µm.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tasmaniae. Its PLS are composed of robust sharply spinulated and pronged spines comparable to those in *T. tasmaniae*, but contrasting to those in *N. americana* (Fig. 9.11I). Two sharply denticulated component teeth comprise its CDLT (Fig. 9.11G), and three isolated and denticulated teeth form the CVLT (Fig. 9.11H).

The foregut features of *Praunus flexuosus* are similar to those found in both *T. tasmaniae* and *P. rufa*. Its fewer ALS (Fig. 9.13F), and the presence of only type 3 spines on the dorsal surface of the laterale are similar to those in *P. rufa*. Its robust PLS (Fig. 9.13I), however, resemble those in *T. tasmaniae*. Its CVLT are clustered, and small blunt denticles are found on the component teeth (Fig. 9.13G). The CDLT of *P. flexuosus* (Fig. 9.13H) is identical to that in *T. tasmaniae* for it comprises three component teeth, two large and one small. The CDP in this species is simple (Fig. 9.13H).

The foregut features of *Praunus neglectus* shown in figure 9.13A-E are very similar to those already described in *P. flexuosus*. *Paramysis nouveli* possesses foregut features (Fig. 9.8 A-D) common in the three standard foreguts. Its few clustered and pronged ALS (Fig. 9.8 A,B), and the presence of only type 3 spines are features shown in the *P. rufa* foregut. The presence of types 3 and 4 spines are similar to those in *A. mixta australis*. The presence of single row of spines on the pinnacle of the anteromedianum, the five (5) component teeth of the CDLT (Fig. 9.8C), and the clustered and sharply denticulated CVLT (Fig. 9.8D) are features shared with *T. tasmaniae*.

Species from the Neritic Waters of Tyrrhenian Sea

Corsica and the Gulf of Naples

Pyroleptomysis rubra and the three *Leptomysis* species share identical features to those in *T. tasmaniae*. The features of *P. rubra* and *L. gracilis* are shown in Figure 9.14. The internal foregut features of *Hemimysis lamornae mediterranea* are similar to those in *T. tasmaniae* except that it bears four component teeth in its CDLT (Fig. 9.9A). Figure 9.6H shows the clustered and sharply denticulated CVLT. The foregut features of the two *Siriella* species closely resemble those in the other *Siriella* species

Figure 9.13 Foregut features of the *Praunus neglectus* (A-E) and *P. flexuousus* (F-I). A. anterodorsal view of left anterior laterale (l) and associated spines (als, types 1, 3, 4, 19), and pf. B. right cvlt. C. lateral view of the cdp. D. right cdlt. E. pls and type 3 spine. F. anterodorsal view of left anterior laterale and associated spines (als, types 1, 4, and 19), and pf. G. left cvlt. H. lateral view of the cdp. I. pls, and type 3 spine. Scale bar: A, C-F = 0.1 mm; B, G, I = 10 μm.

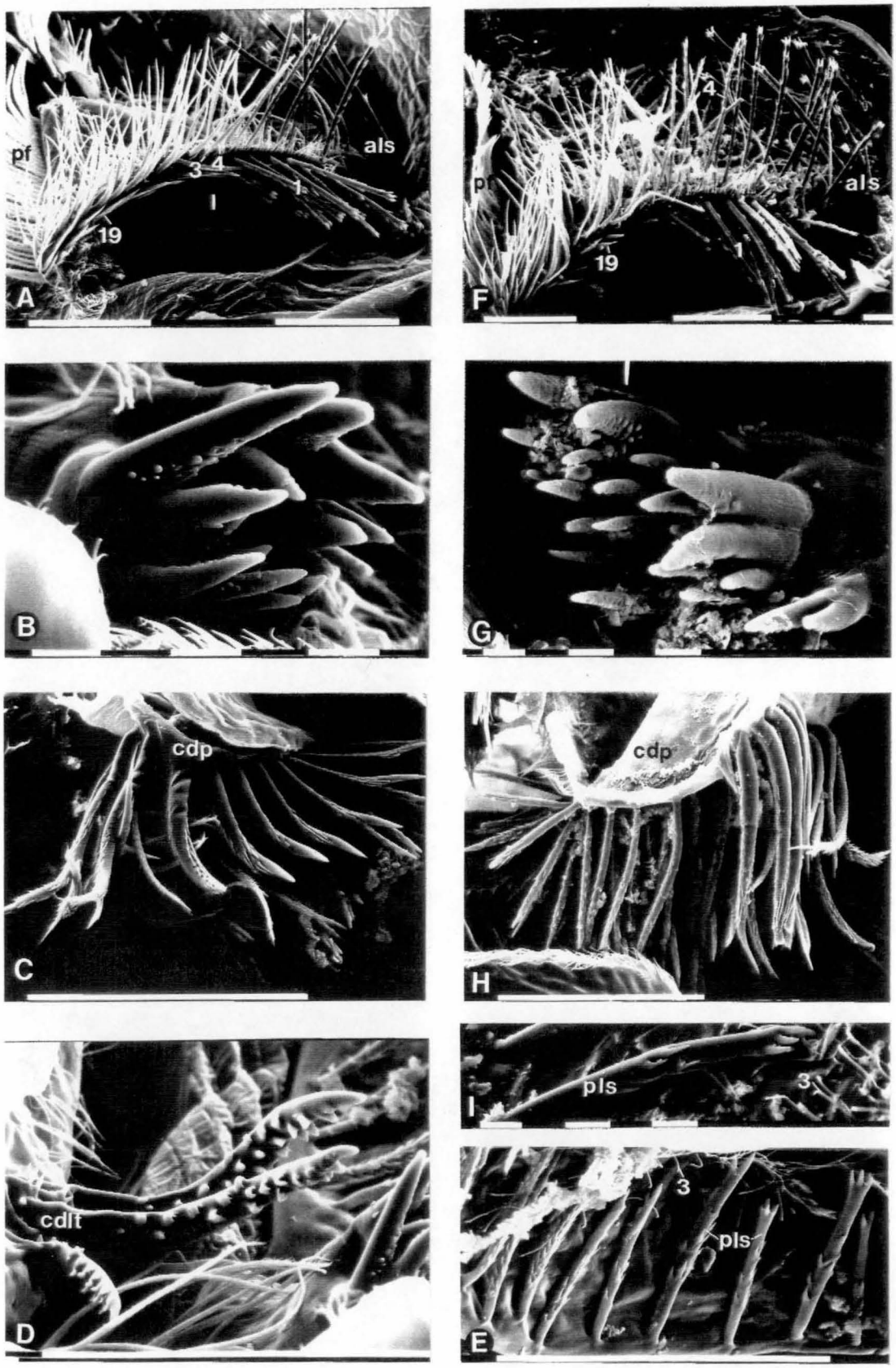
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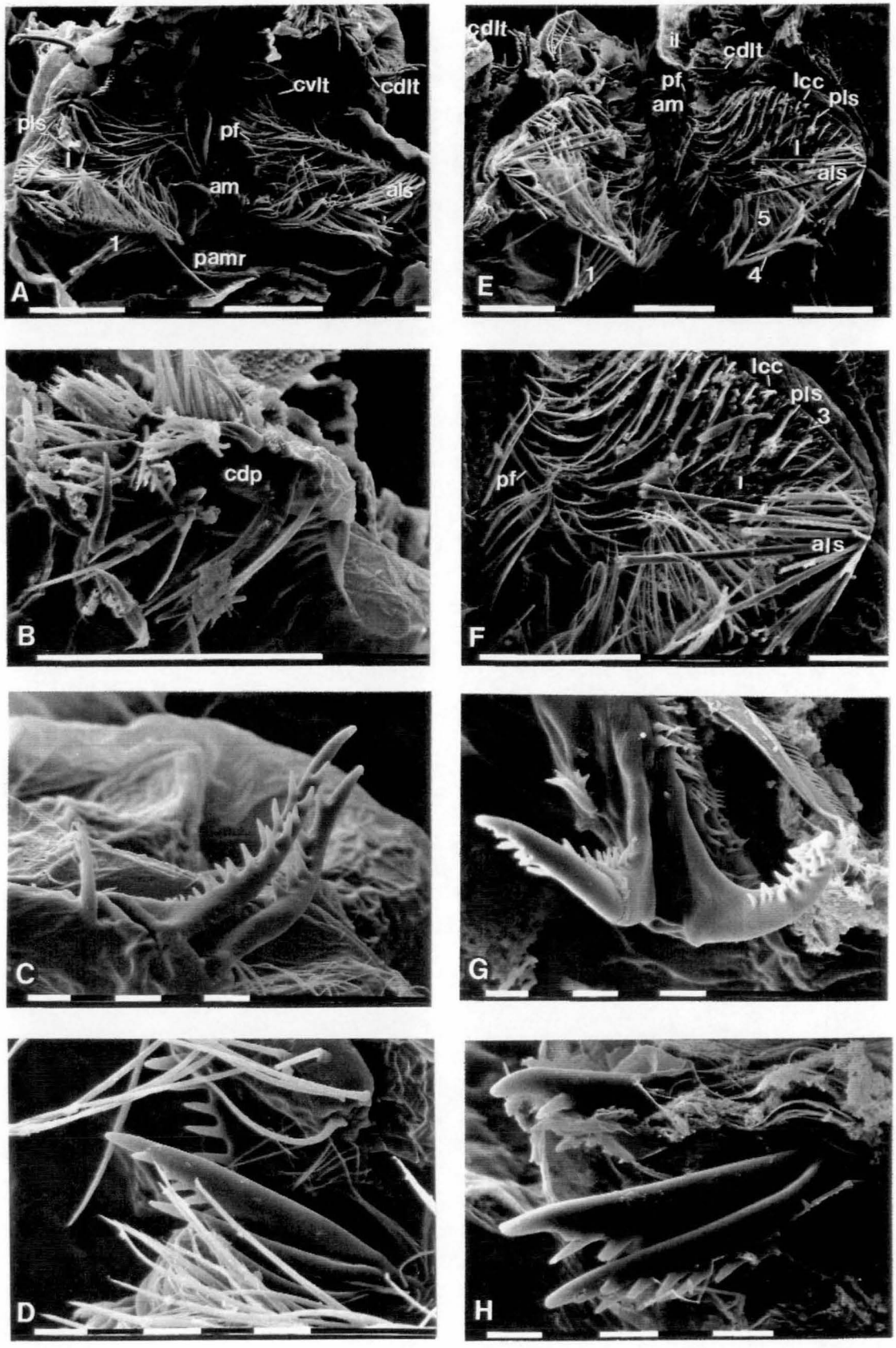
Figure 9.14 Foregut features of *Pyroleptomysis rubra* (A-D), and *Leptomysis gracilis* (E-H). A. anterodorsal view showing laterale (l) and associated spines (als, pls, type 1), am, cdlt, cvlt, pamr, pf. B. left half of cdp. C. left cdlt; D. left cvlt. E. anterodorsal view showing laterale (l) and associated spines (als, pls, types, 1, 4, 5), am, pf, cdlt, cvlt, lcc, il. F. close-up of left lcc, and laterale (l) and associated spines (als, pls, types 3, 5), pf. G. right cdlt. H. left cvlt. Scale bar: A, B, E, F = 0.1 mm; C, D, G, H = 10 μm.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already described. Likewise, the features described in *M. bigelowi* are identical to those in *Mysidopsis gibbosa.*

Gulf of Salerno

The foregut features of *Schistomysis assimilis* are very similar to those species with four CDLT, and these are the two *Hemimysis* species and *Mysis stenolepis* described above. Features in *Paramysis arenosa* are also found in the foregut of its congener, *P. nouveli. Gastrosaccus sanctus*, *Haplostylus bacescui*, and *Haplostylus normani* share features with those *Gastrosaccus* species already described. *H. bacescui* structures are shown in Figures 9.15 A-D.

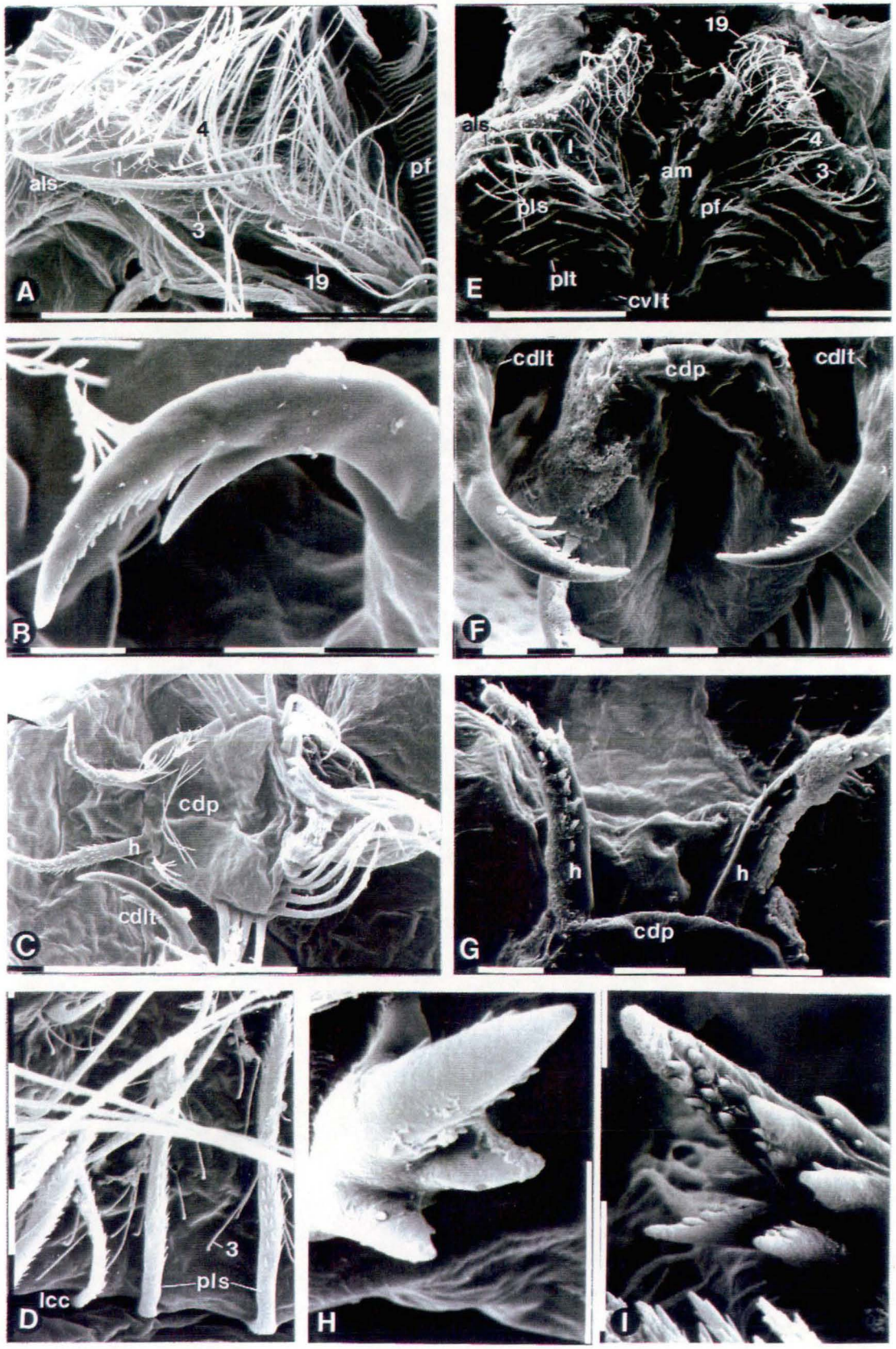
Species from the Coastal Waters of the Adriatic Sea

The foregut features of *Leptomysis buergii*, *L. lingvura adriatica*, *Siriella armata* and *Mesopodopsis slabberi* are very similar to those congeners already described. The tubular foregut of *M. slabberi* is shown in Figure 9.4A, and Figure 9.4B shows the anterodorsal view of the structures of the cardiac region already described in its congener, *M. wooldridgei.* The foregut features of *Acanthomysis longicornis* is similar to those in *T. tasmaniae*, except that its CDLT comprise two component teeth identical to those in the *Neomysis* species, *Erythrops erythropthalma*, and *Nipponomysis lingvura.*

Single Species

Hemimysis speluncula, the marine cave species, shares foregut features with its congener *H. lamornae mediterranea* already described. Likewise, *Gastrosaccus indicus* has features resembling those in the *Gastrosaccus* and *Haplostylus* species. The structures in *G. indicus* are shown in Figure 9.15 E-I. The only non-halophilic species examined, *Limnomysis benedeni*, shares its foregut features with *T. tasmaniae.* The largest of all mysid species examined is *Antarctomysis maxima.* Its foregut features are essentially the same as those found in *T. tasmaniae* in having complex armatures (Figure 9.16). Spine types 1, 3, and 5 form rows on the dorsal

Figure 9.15 Foregut features of *Haplostylus bacescui* (A-D) and *Gastrosaccus indicus* (E-I). A. anterodorsal view of right half of foregut showing the laterale (l) and associated spines (als, types 3,19), pf. B. left cdlt. C. right cdlt, and cdp showing single anterior horn (h). D. pls, type 3 spines, lateral circulation channel (lcc). E. posterodorsal view showing laterale (l) and associated spines (als, pls, types 3, 4, 19) and tooth (plt), am, pf, cvlt. F. anteroventral view of body of cdp, and right and left cdlt. G. anterior pair of single horns of the cdp. H. right cvlt exposing non-denticulated surface. I. left cvlt showing denticulated surface. Scale bar: A, C, E = 0.1mm; B, D, F-I = 10μm.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cdp
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cdp
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cdp
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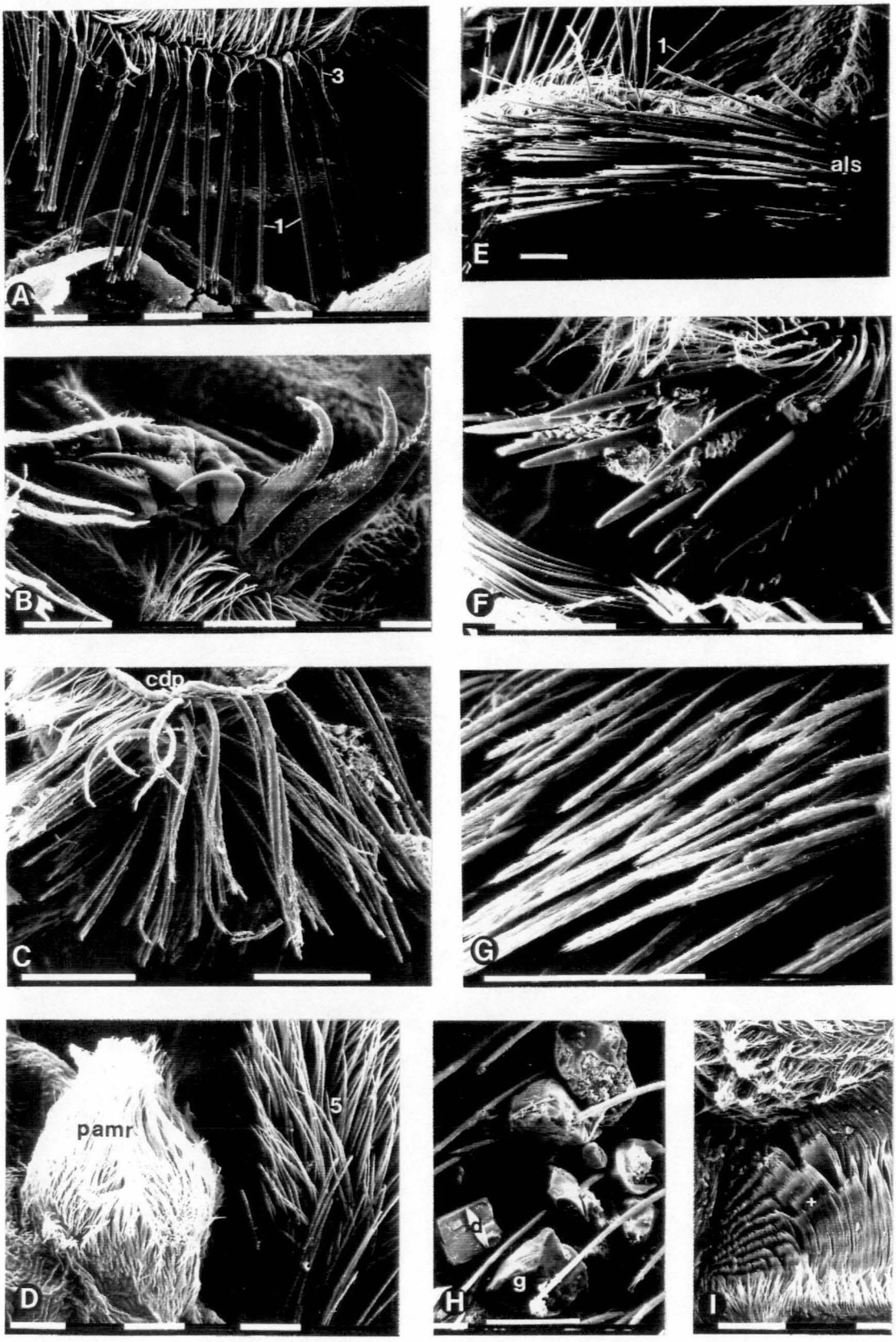
Figure 9.16 Foregut features of *Antarctomysis maxima*. A. Types 1, and 3 spines on laterale. B. left cdlt. C. lateral view of the left half of cdp. D. pamr, and type 5 spines on laterale. E. als, type 1 spine. F. left cvlt. G. left laterale pls. H. type 5 spine, and stomach contents (gastroliths (g), and diatom (d)). I. spines (+) on the inferolateral inner wall opposite to the secondary filter spines. Scale bar: Scale bar: A-G, I = 0.1 mm; H = 44.1 μm.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edge of the anterior laterale (Fig. 9.16A). The ALS is a dense cluster of pronged-tipped spines (Fig. 9.16E). Finely spinulated and unpronged spines form the dense PLS (Fig. 9.16G). The pinnacle of its anteromedianum bears a row of type 20 spines. *A. maxima* possesses a prominent pre-anteromedianum ridge (pamr) in front of the type 5 spine-covered medial surface of the laterale (Fig. 9.16D). Eight denticulated component teeth comprise the CDLT (Fig. 9.16B). The CVLT is clustered and composed of denticulated surfaces, and numerous sharp apices (Fig. 9.16F). The CDP is simple, but bears more dense stout spines than those in *P. rufa* and *T. tasmaniae*. The pyloric chamber also contains similar structures to those found in the three standard foreguts, but its secondary filter is much larger and bears seven rows of the filtering spines (Fig. 9.16I).

Habitat Association and Diet

Table 9.4 shows the size, habitat association, and diet of all mysid species analyzed in the present study. The different species are categorized according to their association with the substrate into pelagic (species inhabiting the water column), hyperbenthic and/or epibenthic (species found on or 1 cm above) the bottom, and benthopelagic (species which burrow in the substrate during the day and swim up in the water column at dusk/night). With the exception of those species which were directly observed *in situ* (*e.g.* the three Tasmanian mysid species), the categories assigned to the other species are tentative.

Dietary information is available for 34 of the mysid species examined and only 18 of these species have diets and feeding behaviour well studied. Although the diet information for the majority of these species indicates omnivorous feeding, three arbitrary classification of feeding habits were established. The species belonging to these categories are the following:

(1) C or carnivores - the reported diets of these species were predominantly animal (mainly crustacean) prey, but species belonging to this category - *Paramesopodopsis rufa, Rhopalophthalmus terranatalis, Siriella longipes, S. anomala, S. armata, Mysis*

Table 9.4 Size, habitat association, and diet of the mysid species analyzed.

Species	Total Length (mm)	Habitat Association
Anisomysis mixta australis	6.0	pelagic, over sand and rock patches
Paramesopodopsis rufa	10.5	pelagic, among rocks with attached seaweeds
Tenagomysis tasmaniae	8.4	benthic, on sandy substrate
Tenagomysis australis	12.7	pelagic, epibenthic
Tasmanomysis oculata	15.5	pelagic
Australomysis acuta	6.2	benthopelagic, clings on surface of kelp
Rhopalophthalmus terranatalis	16.4	pelagic, estuarine, swims ventral side up
Gastrosaccus brevifissura	7.6	bentho-pelagic, burrows in sand
Gastrosaccus psammodytes	14.2	bentho-pelagic, burrows in sand
Mesopodopsis wooldridgei	11.6	pelagic
Anisomysis ijimai	5.7	pelagic, over sand
Nipponomysis lingvura	7.1	benthic, on sand
Siriella longipes	8.8	pelagic, over sand
Gastrosaccus bengalensis	7.3	benthopelagic, on sandy substrates
Siriella anomala	8.4	pelagic, over sandy substrates
Anchialina typica	6.6	benthopelagic
Mysis stenolepis	17.5	pelagic, among *Zostera* beds, shallow subtidal
Mysis mixta	18.5	benthopelagic, on silt-clay sediments
Bowmaniella brasiliensis	7.9	benthopelagic
Mysidopsis bigelowi	3.8	epibenthic, sandy, clayey-silt, shallow shelf
Erythrops erythrophthalma	8.1	epibenthic, sandy sediments with silt
Neomysis americana	12.8	epibenthic, sand associated
Neomysis integer	12.1	benthopelagic, estuarine
Praunus flexuosus	8.4	pelagic, over sand and patches of seaweeds
Praunus neglectus	10.5	pelagic, among seaweeds (*Laminaria* beds)
Paramysis nouveli	8.2	benthic, tide pools with algae and sand
Leptomysis gracilis	8.6	epibenthic, on anemone, rocks, algae, *Zostera*
Leptomysis lingvura marioni	8.9	epibenthic, sandy, rocky, marine caves
Leptomysis posidoniae	7.4	epibenthic, rocks, seagrass: *Posidonia*
Pyroleptomysis rubra	7.8	epibenthic, bentho-pelagic, rocky substrates
Siriella clausii	5.8	pelagic, among weeds, over sand in rock pools
Siriella jaltensis gracilipes	10.5	pelagic, clings on *Zostera*, marine cave dweller
Mysidopsis gibbosa	5.8	benthopelagic, over sand
Hemimysis lamornae mediterranea	4.9	benthic, lives among rocks, clings on seaweed
Gastrosaccus sanctus	9.1	benthopelagic, buries in sand during daytime
Schistomysis assimilis	8.7	epibenthic
Haplostylus bacescui	7.9	bentho-pelagic, on sand
Haplostylus normani	7.1	bentho-pelagic, on sand
Paramysis arenosa	5.6	pelagic, among weeds, sublittoral sandy bays
Leptomysis buergii	9.1	benthic, benthopelagic, mud, biogenic structures
Leptomysis lingvura adriatica	7.6	rocks, algae
Siriella armata	16.3	pelagic, among weeds, clings on *Zostera*
Acanthomysis longicornis	6.0	epibenthic, benthopelagic
Mesopodopsis slabberi	9.5	pelagic
Hemimysis speluncula	6.2	benthopelagic, marine caves
Gastrosaccus indicus	7.8	benthopelagic
Antarctomysis maxima	54.2	hyperbenthic, mesopelagic zone
Limnomysis benedeni	6.0	epibenthic, lakes and rivers

Table 9.4 continuation

Diet (Feeding Habit*)
predominantly fine particulate organic matter; occasional crustacean remains (C - H)†
predominantly crustacean; macroalgal particles (C)†
predominantly macroalgal particles; occasional crustaceans, dinoflagellates (D/H - C)†
daytime: algal detritus (D/H - C)
algal detritus, crustacean remains (D/H - C)
unknown
copepods, juvenile *M. wooldridgei*, phytoplankton, plant debris, detritus (C)†
mainly phytoplankton and detritus (D/H - C)†
detritus (daytime), diatoms and zooplankton (nighttime) (D/H - C)†
calanoid copepods, phytoplankton, extensively on chain-forming diatoms (C-H)†
crustacean remains, diatoms, dinoflagellates, detritus (C-H)†
mainly detritus, diatoms (D/H - C)
mainly zooplanktonic crustaceans (C)
polychaete worm, detritus (D/H - C)
mainly copepod remains (C)
unknown
raw cellulose, particulate organic matter, detritus (D/H - C)†
mainly zooplankton (copepods, cladocerans, tintinnids, rotifers, amphipod) and detritus (C)†
unknown
Centropages spp., mainly small crustaceans (C)
detritus, diatoms, crustacea, faecal pellets, terrigenous material (D/H - C)
organic detritus, smaller crustaceans, diatoms, *Artemia* sp. nauplii, *Acartia tonsa* (D/H - C)†
phytoplankton, terrigenous material, algal fragments; mainly copepods, rotifers, amphipod(C)†
(highly carnivorous) polychaete, calanoid & harpacticoid copepods, contents of *Daphnia* (C)†
copepod crustacean, detritus, algae, terrigenous material (D/H - C)
unknown
detritus, fine particulate matter, terrigenous materials: silt, leaf fragments, spores (D/H - C)
unknown
unknown
fine particulate matter (filter feeding, unspecialized), detritus (D/H - C)†
unknown
unknown
mainly small copepods (voracious carnivore), few dinoflagellates, some silt (C)†
suspended particulate organic matter (D/H - C)
detritus (D/H - C)
unknown
unknown
unknown
small copepod, detritus, silt, diatoms, dinoflagellates, terrigenous materials: spores (D/H - C)†
detritus, fine particulate matter, crustacean remains (D/H - C)
unknown
animal food (C)†
very minute organisms, fine detrital particles (D/H - C)
crustacea, detritus, phytoplankton (C-H)
unknown
unknown
diatoms, copepods, amphipods, nanoplankton, detritus, quartz silt (D/H - C)†
algal detritus (D/H - C)

*C - carnivorous
D/H - detritivorous/herbivorous
†species with well studied diet and feeding behaviour

Table 9.4 continuation

References
Fenton 1986, 1992; present study
Fenton 1986, 1992; present study
Fenton 1986, 1992; present study
Fenton 1986, 1991; present study
Fenton 1986; present study
Fenton 1986; Barrett 1994 (pers. comm); present study
Wooldridge and Bailey 1982; Perrisinotto *et al.* 1987
Wooldridge and Bailey 1982
Wooldridge 1981; Wooldridge 1983; Webb *et al.* 1988; Wooldridge 1989
Wooldridge and Bailey 1982; Wooldridge 1983; Webb *et al.* 1987; Webb and Wooldridge 1990
Ii 1964; Fukuoka 1994 (pers. comm.)
Takahashi and Murano 1986; Fukuoka 1994 (pers com)
Ii 1964; Fukuoka 1994 (pers com)
Hansen 1910; Ii 1964; Tattersall 1951; Murano 1983
Hansen 1910; Ii 1964; Tattersall 1951
Tattersall 1951
Wigley and Burns 1971; Foulds and Mann 1978; Maurer and Wigley 1982; Corey 1988
Wigley and Burns 1971; Mauchline 1980; Rudstam *et al.* 1989; Rudstam and Hansson 1990
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Tattersall 1951; Mauchline 1971c, 1980; Ariani *et al.* 1993
Tattersall 1951; Mauchline 1971c, 1980; Ariani *et al.* 1993
Ariani *et al.* 1993
Mauchline 1980; Wittmann 1978; Ariani *et al.* 1993
Mauchline 1969, 1971, 1977, 1980; Wittmann 1977, 1978; Ariani *et al.* 1993
Tattersall and Tattersall 1951; Mauchline 1971; Wittmann 1977; Ariani *et al.* 1993
Wittmann 1985; Ariani *et al.* 1993
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Ariani *et al.* 1993
Tattersall and Tattersall 1951; Mauchline 1980; Ariani *et al.* 1993
Tattersall and Tattersall 1951; Moran 1972; Hamond 1974; Wittmann 1977; Ariani *et al.* 1993
Ariani *et al.* 1993
Tattersall and Tattersall 1951; Mauchline 1971b, 1980; Ariani *et al.* 1993
Ariani *et al.* 1993
Wittmann 1977; Ariani *et al.* 1993
Tattersall and Tattersall 1951; Wittmann 1977; Mayzaud 1986; Ariani *et al.* 1993
Tattersall and Tattersall 1951; Ariani *et al.* 1993
Ariani *et al.* 1993
Mauchline 1980; Ariani *et al.* 1993
Hansen 1910; Ii 1964; Ariani *et al.* 1993
Mauchline 1980; Siegel and Mühlenhardt-Siegel 1988; Ariani *et al.* 1993
Mauchline 1980; Ariani *et al.* 1993

mixta, the two *Mysidopsis* species (*bigelowi* and *gibbosa*), *Praunus flexuosus* and *Neomysis integer* - might either be facultative or obligate.

(2) C-H or carnivore-herbivore - the diet is characterized by mainly animal prey and fine particulate matter (chain forming diatoms). *Anisomysis mixta australis*, *A. ijimai*, *Mesopodopsis wooldridgei*, and *M. slabberi* belong to this category.

(3) D/H-C or detritivore/herbivore-carnivore - diet is dominated by algal detritus, terrigenous materials, and occasional crustacean or animal prey. The remainder of the 33 species belong to this category: the two *Tenagomysis* species (*tasmaniae* and *australis*), *Nipponomysis lingvura*, *Mysis stenolepis*, *Hemimysis lamornae mediterranea*, *Antarctomysis maxima*, *Acanthomysis longicornis*, *Limnomysis benedeni*, *Pyroleptomysis rubra*, the two *Leptomysis* species (*bürgii* and *gracilis*), the four *Gastrosaccus* species (*brevifissura*, *psammodytes*, *bengalensis*, *sanctus*), *Erythrops erythrophthalma*, *Neomysis americana*, *Praunus neglectus*, and *Paramysis arenosa*.

The Phylogenetic Tree

Table 9.5 shows the 25 characters used in the PAUP analysis. All of these characters were treated as ordered following the Wagners parsimony using binary (presence -absence) characters which are allowed to change irreversibly (Swofford 1991). The data matrix is presented in Table 9.6, and it may be appended for future phylogenetic studies which use other mysid characters.

Ordinary Heuristic Search

Figure 9.17 shows the unrooted tree (Tree length = 50, Consistency Index (CI) = 0.5, Homoplasy Index (HI) = 0.5, Retention Index (RI) = 0.857) computed by PAUP. The tree suggests two sister groups: the first comprising *Rhopalophthalmus terranatalis* and members from the sub-family Gastrosaccinae, and the second group is composed of the rest of the species examined. All species from the *Haplostylus*, *Bowmaniella*, and *Gastrosaccus* genera were unresolved, as were *R. terranatalis* and

Table 9.5 Characters and Character states of the foregut used in the cladistic analysis. All characters were treated as ordered.

Characters	States
1. Foregut type	0 - spheroidal; 1 - tubular
2. Roof of cardiac chamber	0 - unfolded; 1- dorsoventrally folded
3. Anterior laterale spines (ALS)	0 - present; 1 - absent
4. ALS disposition	0 - clustered; 1 - unclustered
5. Posterolaterale spines (PLS)	0 - present; 1 - absent
6. PLS type	0 - pronged; 1 - unpronged
7. PLS spinnulation	0 - robust; 1 - not robust
8. Posterior laterale tooth (PLT)	0 - present; 1 - absent
9. Laterale surface	0 - type 3 + other spines; 1 - type 3 only
10. Anterior laterale spines	0 - all types present; 1 - not all types present
11. Cardiac dorsal piece(CDP)	0 - present; 1 - absent
12. CDP type	0 - unhorned, simple; 1 - horned, compound
13. Primary filter	0 - closely gapped, elaborate spinulation; 1 - widely gapped, less spinulated
14. Anteromedianum long spines	0 - single row ; 1 - patch
15. Cardiac dorsolateral teeth(CDLT)	0 - present; 1 - absent
16. CDLT 1+0 dentition formula (df)	0 - present; 1 - absent
17. CDLT 2+0 df	0 - present; 1 - absent
18. CDLT 2+1 df	0 - present; 1 - absent
19. CDLT 2+2 df	0 - present; 1 - absent
20. CDLT 2+3 df	0 - present; 1 - absent
21. CDLT 3+0 df	0 - present; 1 - absent
22. CDLT 3+3+2 df	0 - present; 1 - absent
23. Cardiac ventrolateral teeth (CVLT)	0 - present; 1 - absent
24. CVLT disposition	0 - clustered; 1 - unclustered
25. CVLT denticulation	0 - denticulated; 1 - non-denticulated

Table 9.6 Matrix of taxa and character states used in the PAUP analysis. See Table 9.5 for details of each character and states, and Table 9.7 for taxon abbreviation.

	Character																								
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Taxon																									
Rhopaloter	0	0	0	1	0	1	?	0	1	1	0	1	0	0	0	1	1	1	1	1	0	0	0	1	0
Anchialitypi	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	1	0	1	1	1	1	1	0	0	0
Acanthlong	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	1	1	1	1	1	0	1	0
Anisoijimai	0	0	0	1	0	0	0	1	1	1	0	0	0	1	0	0	1	1	1	1	1	1	0	0	0
Anisomixau	0	0	0	1	0	0	0	1	1	1	0	0	0	1	0	0	1	1	1	1	1	1	0	0	0
Antarctmax	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0
Australoacut	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	1	1	0	0	0
Bowmanbra	0	0	0	1	0	1	1	0	0	1	0	1	0	0	0	0	1	1	1	1	1	1	0	0	0
Erythroeryth	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	0	1	1	1	1	1	0	1	0
Gastrosbeng	0	0	0	1	0	1	1	0	0	1	0	1	0	0	0	0	1	1	1	1	1	1	0	0	0
Gastrosbrev	0	0	0	1	0	1	1	0	0	1	0	1	0	0	0	0	1	1	1	1	1	1	0	0	0
Gastrosindi	0	0	0	1	0	1	1	0	0	1	0	1	0	0	0	0	1	1	1	1	1	1	0	0	0
Gastrospsam	0	0	0	1	0	1	1	0	0	1	0	1	0	0	0	0	1	1	1	1	1	1	0	0	0
Gastrossanc	0	0	0	1	0	1	1	0	0	1	0	1	0	0	0	0	1	1	1	1	1	1	0	0	0
Haplostybac	0	0	0	1	0	1	1	0	0	1	0	1	0	0	0	0	1	1	1	1	1	1	0	0	0
Haplostynor	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	0	1	1	1	1	1	1	0	0	0
Hemimylam	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	1	0	1	1	1	0	0	0
Hemimyspe	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	1	0	1	1	1	0	0	0
Leptombür	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0	0	0
Leptomgra	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0	0	0
LeptomliA	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	1	1	0	1	1	1	1	0	0	0
LeptomliM	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0	0	0
Leptompos	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0	0	0
Limnomben	0	0	0	1	1	?	?	1	1	1	0	0	0	0	0	1	1	0	1	1	1	1	0	0	0
Mesopsla	1	0	1	?	1	?	?	1	?	1	1	?	1	?	1	?	?	?	?	?	?	?	1	?	?
Mesopwol	1	0	1	?	1	?	?	1	?	1	1	?	1	?	1	?	?	?	?	?	?	?	1	?	?
Mysidopbig	0	0	0	1	1	?	?	1	1	1	0	?	0	?	0	0	1	1	1	1	1	1	0	0	0
Mysidopgib	0	0	0	1	1	?	?	1	1	1	0	?	0	?	0	0	1	1	1	1	1	1	0	0	0
Mysismixta	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	1	1	1	0	1	1	0	0	0
Mysissteno	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	1	1	0	1	1	1	0	0	0
Neomysame	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	1	1	1	1	1	0	1	0
Neomysisint	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	1	1	1	1	1	0	1	0
Nipponling	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	0	1	1	1	1	1	0	1	0
Paramesoruf	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	1	0	0	1
Paramysare	0	0	0	1	1	?	?	1	1	1	0	0	0	0	0	1	1	1	1	0	1	1	0	0	0
Paramysnou	0	0	0	1	1	?	?	1	1	1	0	0	0	0	0	1	1	1	1	0	1	1	0	0	0
Praunusflex	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	1	1	1	1	0	0	0
Praunusneg	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	1	1	1	1	0	0	0
Pyroleptrub	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0	0	0
Schistoass	0	0	0	1	0	1	?	0	1	1	0	1	0	0	0	1	1	1	0	1	0	0	0	1	0
Siriellaarm	0	0	0	0	1	?	?	1	1	1	0	0	0	0	0	0	1	1	1	1	1	1	0	1	0
Siriellaano	0	1	0	1	1	?	?	1	1	1	0	0	0	?	0	0	1	1	1	1	1	1	0	0	1
Siriellaclau	0	1	0	1	1	?	?	1	1	1	0	0	0	?	0	0	1	1	1	1	1	1	0	0	1
Siriellajagra	0	1	0	1	1	?	?	1	1	1	0	0	0	?	0	0	1	1	1	1	1	1	0	0	1
Siriellalon	0	1	0	1	1	?	?	1	1	1	0	0	0	?	0	0	1	1	1	1	1	1	0	0	1
Tasmanocu	0	0	0	1	0	1	0	1	1	1	0	0	0	0	0	1	1	0	1	1	1	1	0	0	0
Tenagoaust	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0	0	0
Tenagotas	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0	0	0

Table 9.7 Species names for the taxon abbreviation in Table 9.5.

Taxon Abbreviation	Species Name
Rhopaloter	*Rhophalophthalmus terranatalis*
Anchialitypi	*Anchialina typica*
Acanthlong	*Acanthomysis longicornis*
Anisoijimai	*Anisomysis ijimai*
Anisomixau	*Anisomysis mixta australis*
Antarctmax	*Antarctomysis maxima*
Australoacut	*Australomysis acuta*
Bowmanbra	*Bowmaniella brasiliensis*
Erythroeryth	*Erythops erythrophthalma*
Gastrosbeng	*Gastrosaccus bengalensis*
Gastrosbrev	*Gastrosaccus brevifissura*
Gastrosindi	*Gastrosaccus indicus*
Gastrospsam	*Gastrosaccus psammodytes*
Gastrossanc	*Gastrosaccus sanctus*
Haplostybac	*Haplostylus bacescui*
Haplostynor	*Haplostylus normani*
Hemimylam	*Hemimysis lamornae mediterranea*
Hemimyspe	*Hemimysis speluncula*
Leptombür	*Leptomysis bürgii*
Leptomgra	*Leptomysis gracilis*
LeptomliA	*Leptomysis lingvura adriatica*
LeptomliM	*Leptomysis lingvura marioni*
Leptompos	*Leptomysis posidoniae*
Limnomben	*Limnomysis benedeni*
Mesopsla	*Mesopodopsis slabberi*
Mesopwol	*Mesopodopsis wooldridgei*
Mysidopbig	*Mysidopsis bigelowi*
Mysidopgib	*Mysidopsis gibbosa*
Mysismixta	*Mysis mixta*
Mysissteno	*Mysis stenolepis*
Neomysame	*Neomysis americana*
Neomysisint	*Neomysis integer*
Nipponling	*Nipponomysis lingvura*
Paramesoruf	*Paramesopodopsis rufa*
Paramysare	*Paramysis arenosa*
Paramysnou	*Paramysis nouveli*
Praunusflex	*Praunus flexuosus*
Praunusneg	*Praunus neglectus*
Pyroleptrub	*Pyroleptomysis rubra*
Schistoass	*Schistomysis assimilis*
Siriellaarm	*Siriella armata*
Siriellaano	*Siriella anomala*
Siriellaclau	*Siriella clausi*
Siriellajagra	*Siriella jaltensis gracilipes*
Siriellalon	*Siriella longicornis*
Tasmanocu	*Tasmanomysis oculata*
Tenagoaust	*Tenagomysis australis*
Tenagotas	*Tenagomysis tasmaniae*

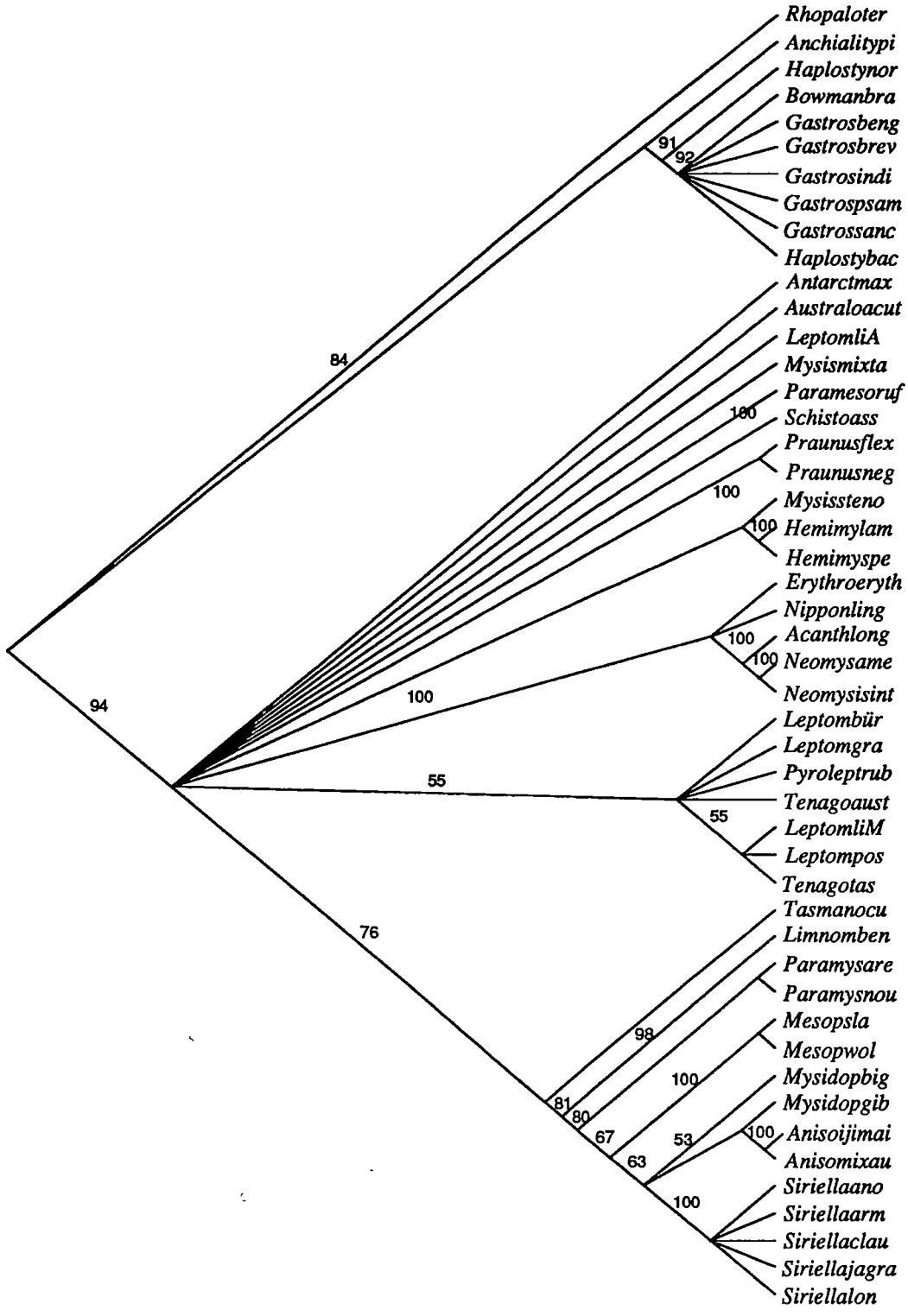

Figure 9.17 Majority-rule (50%) consensus. See Table 9.7 for taxon abbreviation. Processing time = 84 h.

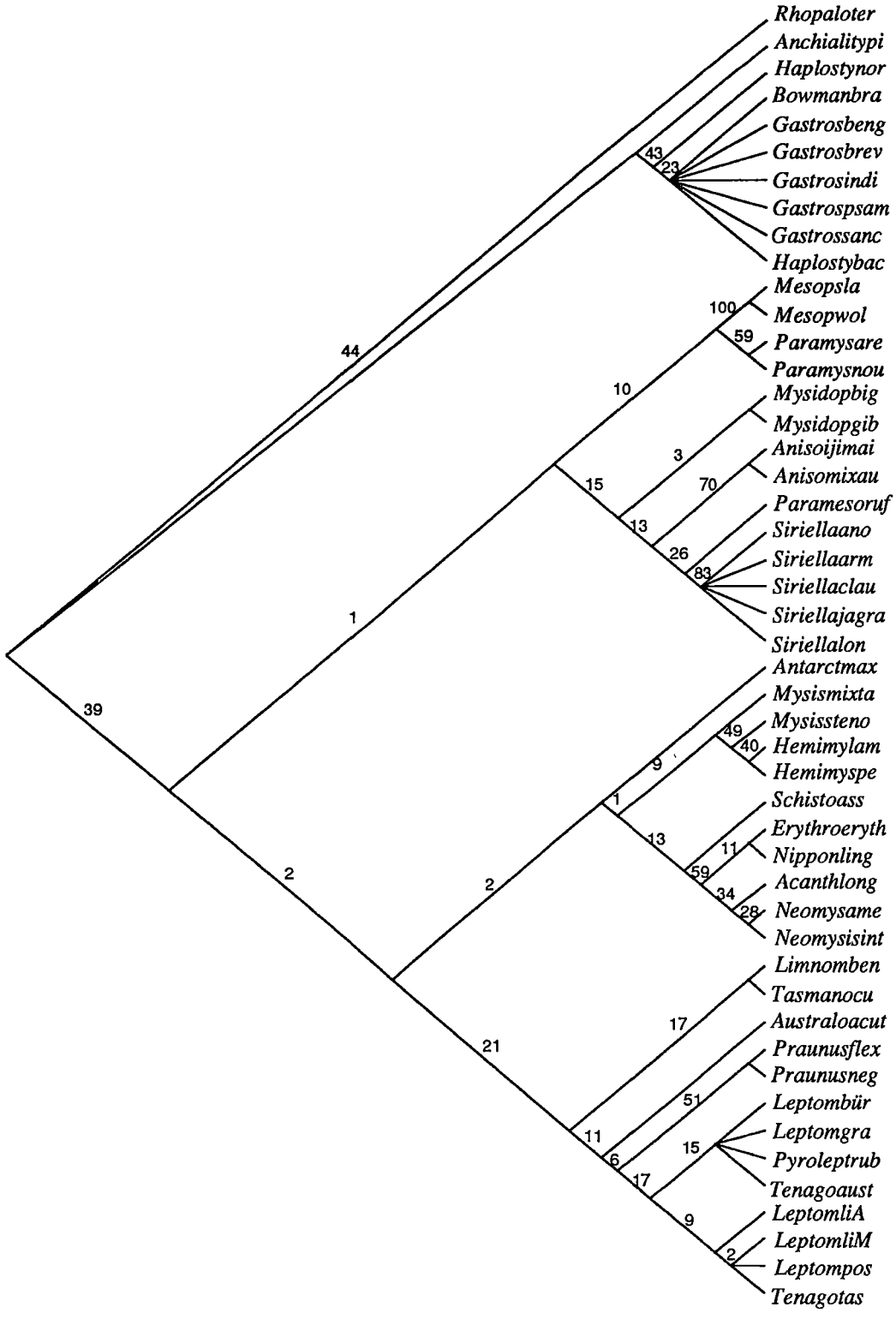

Figure 9.18 Majority-rule (50%) consensus by bootstrapping. See Table 9.7 for taxon abbreviation. Processing time = 84 h.

Anchialina typica. The three characters which distinguish the first group are the unclustered ALS, the presence of PLT, and the compound CDP with anterior horns.

The members of the other sister group possess the simple unhorned CDP, the clustered ALS, and the absence of PLT. Within this lineage, loss and modification of spines on the laterale, and the cardiac dorsolateral teeth (CDLT) dentition formula (df) are the variable characters which separate species from each other. The majority of species in this lineage show foregut features with the laterale bearing the complete spine types observed in *Tenagomysis tasmaniae*, and other members of the Tribe Leptomysini. These include the *Leptomysis* and *Tenagomysis* genera. Although the genera including *Mysis*, *Antarctomysis*, *Tasmanomysis*, *Limnomysis*, *Praunus*, and *Australomysis* share the 2+1 CDLT df as those in the Leptomysini tribe, species within these genera have lost spine types on the edge of the anterior laterale, have only type 3 spines on the dorsal surface of the laterale, and a less robust PLS. The latter two changes are also shown in *Paramesopodopsis rufa*. This species shares with the Leptomysini group the complete spine types on the anterior laterale and the dense ALS cluster. However, instead of bearing the 2+1 df, two of these teeth (1 small and 1 large) are lost, thus the change to 1+0 CDLT df. In addition, the single row of type 20 spines on the anteromedianum is replaced by a patch formation of the same spine type.

The other modifications include a reduced number of the clustered ALS, and the loss of the small CDLT tooth (2+0 df, viz., *Acanthomysis longicornis*, *Erythrops erythropthalma*, *Neomysis integer*, and *N. americana*), the addition of one more of the small spine (2+2 df, e.g. *Mysis stenolepis*, *Hemimysis lamornae*, *H. speluncula*, *Schistomysis assimilis*) and the addition of 2 more of the small spines (2+3 df, e.g. *Paramysis arenosa*, and *P. nouveli*, and *Mysis mixta)*.

Specialization has occurred through the loss of many spines on the laterale, *e.g.* spines being replaced with more powerful teeth (e.g. *Mysidopsis bigelowi* and *M. gibbosa*). Identical to that in *P. rufa*, *Anisomysis mixta australis* and *A. ijimai* possess a patch of spines on the anteromedianum. In *Anisomysis*, one large and one small CDLT teeth are lost leaving the single tooth for its dentition formula (1+0). The

ALS in this genus is unclustered and its PLS have become tooth-like (pronged). As in the *Anisomysis* genus, the *Siriella* genus bears the unclustered ALS, and the 1+0 df. However, members of this genus have lost their PLS, and some of the spine types on the anterior laterale. Only type 3 spines are found on the dorsal surface of their laterale. Another specialization in their foregut is the presence of an anterodorsal invagination in the roof of the cardiac chamber. Their CVLT is devoid of denticulations as found in *P. rufa*. *Mesopodopsis slabberi* and *M. wooldridgei* are two species with the highly derived tubular foregut. The CVLT, CDLT, and CDP are lost. Except for the spines fringing the medial edge of the laterale, all of the spine types are lost on the laterale.

Bootsrapping by Heuristic Search

The phylogenetic tree computed by bootstrapping is shown in Figure 9.18. The concensus tree (Tree length = 53; CI = 0.5, HI = 0.6, RI = 0.832) after the simulation shows almost identical topology with that in the ordinary heuristic search. Two sister groups are also suggested and there are similar unresolved taxa (*Bowmaniella brasiliensis*, *Haplostylus bacescui* and all *Gastrosaccus* species; all *Siriella* species; *Leptomysis bürgii*, *L. gracilis*, *Pyroleptomysis rubra*, and *L. lingvura marioni*, *L. posidoniae*, and *Tenagomysis tasmaniae*). Although some of the unresolved species in the ordinary heuristic search were resolved after bootstrapping, the < 50 % probability (P) values suggest weak resolution of these taxa.

Mysid Foregut Types and Morphocline

Table 9.8 lists the different foregut types of all mysid species examined. The spheroidal foregut (types Ia, Ib, and Ic) shown by the three standard species are found in 46 of the mysid species analyzed. Two species which belong to the *Mesopodopsis* genus show an entirely different tubular foregut or type II. Some of these sympatric species have identical foregut types, for instance, the two species from northwest Philippines have the foregut type Ia. Similarly, the two *Gastrosaccus* species from

Table 9.8 Foregut types of the mysid species analyzed.

Species	Foregut Type
Anisomysis mixta australis	Ia
Paramesopodopsis rufa	Ib
Tenagomysis tasmaniae	Ic
Tenagomysis australis	Ic
Tasmanomysis oculata	Ia
Australomysis acuta	Ic
Rhopalophthalmus terranatalis	Ia
Gastrosaccus brevifissura	Ia
Gastrosaccus psammodytes	Ia
Mesopodopsis wooldridgei	II
Anisomysis ijimai	Ia
Nipponomysis lingvura	Ic
Siriella longipes	Ia
Gastrosaccus bengalensis	Ia
Siriella anomala	Ia
Anchialina typica	Ia
Mysis stenolepis	Ic
Mysis mixta	Ic
Bowmaniella brasiliensis	Ia
Mysidopsis bigelowi	Ia
Erythrops erythrophthalma	Ic
Neomysis americana	Ic
Neomysis integer	Ic
Praunus flexuosus	Ib
Praunus neglectus	Ib
Paramysis nouveli	Ic
Leptomysis gracilis	Ic
Leptomysis lingvura marioni	Ic
Leptomysis posidoniae	Ic
Pyroleptomysis rubra	Ic
Siriella clausii	Ia
Siriella jaltensis gracilipes	Ia
Mysidopsis gibbosa	Ia
Hemimysis lamornae mediterranea	Ic
Gastrosaccus sanctus	Ia
Schistomysis assimilis	Ic
Haplostylus bacescui	Ia
Haplostylus normani	Ia
Paramysis arenosa	Ic
Leptomysis buergii	Ic
Leptomysis lingvura adriatica	Ic
Siriella armata	Ia
Acanthomysis longicornis	Ic
Mesopodopsis slabberi	II
Hemimysis speluncula	Ic
Gastrosaccus indicus	Ia
Antarctomysis maxima	Ic
Limnomysis benedeni	Ic

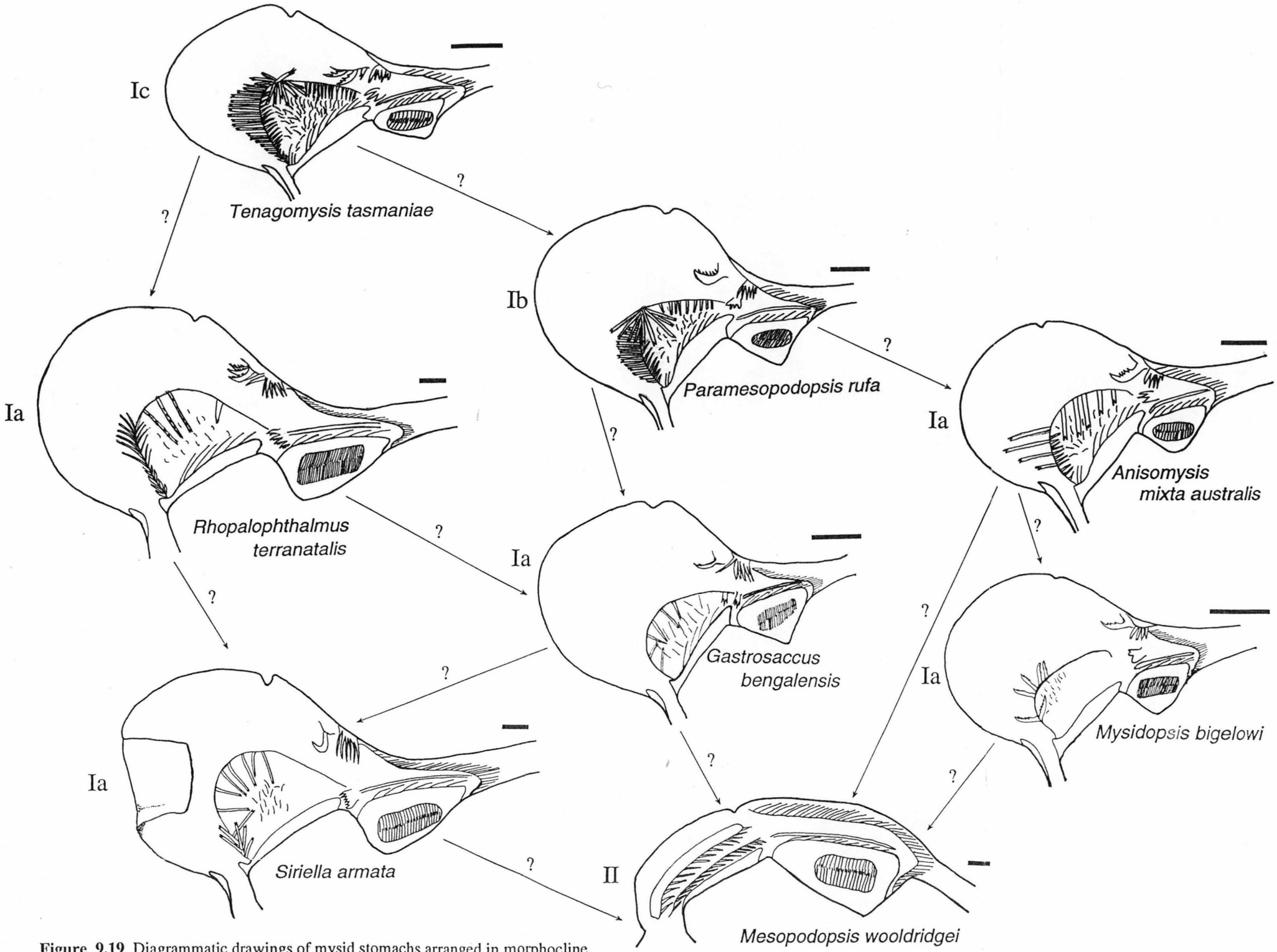

Figure 9.19 Diagrammatic drawings of mysid stomachs arranged in morphocline. The trend from *Tenagomysis tasmaniae* (foregut type Ic) to *Mesopodopsis wooldridgei* (foregut type II) is that of the reduction in number of spines in the cardiac chamber, and the change from spheroidal to tubular shape. ? represents hypothetical evolutionary transformations of mysid foregut morphology. Horizontal scale bars = 0.1 mm.

South Africa have the same foregut type. These two, however, differ in size (Table 9.4). The same is true of the three coexisting Japanese mysid species. *Siriella longipes* and *Anisomyis ijimai* have similar foregut type (type Ia), but the third species, *Nipponomyis lingvura*, has type Ic foregut.

The morphocline (*sensu* Coleman 1994) of the foreguts examined is shown in Figure 9.19. This morphocline does not suggest trends in feeding habits, but represents a series that exhibits a reduction in the number of spines and teeth on the ridges of the cardiac region. The type Ic which is characterized by the most elaborate armature may have directly evolved to type Ia as shown by the foregut of *Rhopalophthalmus terranatalis* via the loss of spine types on the anterior edge of the laterale and the transformation of clustered to isolated anterior lateral spines (ALS). Features of type Ic still retained by this foregut type are the > 1 (3+0 df) CDLT and the posterolateral tooth which might have originated from the robust posterolateral spine (PLS) shown by *T. tasmaniae*. *R. terranatalis* foregut type may have given rise to the type Ia shown by *Siriella*. However, this transformation may have occurred via the transformation of type Ic to the type Ia shown by *P. rufa*, because *Siriella* shares with *P. rufa* the single CDLT (1+0 df), while *P. rufa* still retains the clustered ALS. The type Ia foregut shown by *Gastrosaccus* may be intermediate between *P. rufa* and *Siriella*. The foregut type shown by *P. rufa* may have again become the pivotal point of transformation from type Ia to type Ic shown by *Anisomysis*. The evidence to support this pathway is the fact that *P. rufa* and *Anisomysis* foreguts share the patch formation of spines on the pinnacle of the anteromedianum and the single CDLT (1+0 df). The type Ic shown by *Mysidopsis* may be an extreme case of specialization as spines on the edge of the anterior laterale and the ALS are transformed into tooth-like structures. The tubular foregut (type II: *Mesopodopsis* species) could have originated from four possible ancestral types as suggested by the estimated phylogenetic tree.

Discussion

In the present study the distinction between plesiomorphic/ancestral and

apomorphic/derived foregut characters are based upon the assumptions of Kluge and Farris (1969 cited in Felgenhauer and Abele 1989). They proposed that the primitive features of the crustacean foregut show characters that are: (1) likely to be present in closely related groups; (2) widespread throughout the group; and (3) associated with other character states thought to be primitive based on other evidence. The conserved characters which place all species analyzed as monophyletic are the presence of anteromedianum, laterale, the primary filter in the cardiac chamber, and the ridges and spines in the pyloric chamber and the secondary filter. The presence of the secondary filter suggests the close relationship of mysids with the other peracarids and higher decapods (Gelderd 1909; Haffer 1965; Storch 1986). The spheroidal foregut shape shown by 46 species analyzed may be interpreted as ancestral whereas the tubular form may be a highly derived state. Both PAUP's simple heuristic search- and bootstrapping-generated phylogenetic tree have suggested this interpretation, with the two *Mesopodopsis* species bearing the latter foregut type appearing as a highly resolved taxonomic unit in the second main clade of the tree. The spines on the laterale, the cardiac dorsolateral and ventrolateral teeth, and the cardiac dorsal piece are characters shared by all species with the spheroidal foregut type. Variations such us the integrity and density of these armatures differ between species and it is in these details that diet and/or feeding adaptation may exert a strong influence.

The phylogenetic tree generated in the present study renders the current taxonomic classification of mysids in the Sub-Family Mysinae (Table 9.1) artificial, and comprises paraphyletic tribes. For instance, the Tribe Leptomysini characterized in the present study by the presence of the 2+1 CDLT dentition formula not only includes the genera *Tenagomysis*, *Leptomysis*, and *Pyroleptomysis*, but also *Australomysis*, *Tasmanomysis*, *Praunus*, and *Limnomysis* which all belong to the Tribe Mysini. Conversely, the genus *Mysidopsis* may not belong to the Tribe Leptomysini as shown in the current sytematics, as it possesses the 1+0 dentition formula, type 20 spines on the pinnacle of the anteromedianum, and an unclustered ALS. The obvious differences in the foregut features of the genera *Paramesopodopsis* and *Mesopodopsis* raise the taxonomic question whether the name of the former genus

is appropriate. The genus *Paramesopodopsis* in the Tribe Mysini may have to be renamed. *Paramesopodopsis* shows very similar features with *Halemysis* which also belongs to the Tribe Mysini (Fenton 1986). Until the foregut features of *Halemysis* are examined and compared with those of *Paramesopodopsis*, the latter genus should have a provisional new name. As an alternative I am proposing the new genus *Fentoniella* after Dr. Gwen Fenton who erected the genus *Paramesopodopsis* in 1985.

Phylogenetic history may not strictly determine possible feeding adaptations, as within lineages, change to a different feeding strategy may independently arise, perhaps due to drift or internal genetic or developmental factors. This is shown in the case of *P. rufa* which shows affinity with the Tribe Leptomysini, or those species which show foregut features which have great potential for feeding on tough detrital materials (*e.g.* algal detritus), or potential herbivores. Phylogeny seems to strongly suggest that *P. rufa* should have a greater tendency to display the "ideal" feeding adaptation, but it differs from other members of the detritivorus grade, in that it has a strong predilection to carnivorous or necrophagous feeding. Perhaps the influence of phylogeny may still be manifested because, had it not been for some of the features inherited by *P. rufa* (*e.g.* the presence of the clustered ALS), adaptation for feeding on large and bulky animal prey would not have been possible.

The evidence shown in mysid foreguts suggests that food gathering might have been such a strong selective force that feeding adaptations mask the phylogeny of the different species examined.

The morphocline of the mysid foregut structure proposed in the present study does not necessarily mean that the trend from a highly complex gastric armature shown by the foregut type Ic, the intermediate foregut type Ib and type Ic, to the tubular and highly simplified foregut type II reflects detritivorous/herbivorous to carnivorous feeding habit. Species having the type Ia foregut show the three feeding habits of predominantly carnivorous (*Rhopalophthalmus terranatalis*, *Mysidopsis* species, and the *Siriella* species), fine particulate (*Anisomysis* species), and omnivorous (*Gastrosaccus* species) diets. The distinctive invagination in the roof of the cardiac chamber in *Siriella* may be an adaptive feature for storing large animal prey

as noted in euphausiids (Nemoto 1977) and amphipods (Sheader and Evans 1977; Coleman 1994). The omnivorous feeding habits of *Gastrosaccus* may be tightly linked to its pronounced diel behaviour of staying partially buried during daytime in the sand where it could ingest mainly detrital particles accumulated on the substrate and swimming up in the water column at night where it can suspension feed on zooplankton (Wooldridge 1981). The foregut type Ib is adapted to cope with a carnivorous diet as shown by *Paramesopodopsis rufa* , *Praunus flexuosus*, and *Mysis mixta*, and a detritivorous/herbivorous diet as exhibited by *Praunus neglectus*, *Paramysis arenosa*, and *Mysis stenolepis*. With the exception of *Neomysis integer* because of its carnivorous feeding habit, species which possess the foregut type Ic (*Tenagomysis* species, *Nipponomysis lingvura*, *Neomysis americana*, *Erythrops erythrophthalma*, *Leptomysis species*, *Pyroleptomysis rubra*, *Limnomysis benedeni*, *Antarctomysis maxima*, *Acanthomysis longicornis*, and *Hemimysis lamornae mediterranea*) are predominantly detritivorous and/or herbivorous. Types Ib and c, as already mentioned in chapter 9, are therefore best adapted to coping with large and bulky food. The tubular foregut shown by the two *Mesopodopsis* species may be a specialization to fine particles suspension feeding as in *Anisomysis* species (foregut type Ia), and/or suction feeding on live and decomposing animal prey. This interpretation of the feeding adaptations in *Mesopodopsis* is further supported by the coarse primary filter which is formed by a widely spaced and short spinulated row of filter spines.

A weak point in trying to relate feeding morphology with ecology in the mysid species examined is that diet of many of them has not been established. Added to this is the fact that the basic feeding habit in mysids is omnivory (Mauchline 1980) which requires a detailed analysis of dietary items to quantify the relative importance of each. As in copepods (Paffenhøffer 1988), mysids species may have varying propensities to a particular diet. Mauchline (1989) noted that most euphausiids are omnivorous, but a few are strictly herbivorous or carnivorous at least during certain seasons of the year. Diet should therefore be analyzed in detail taking into consideration the variation of food type, quality and quantity over time. Except for the Tasmanian, South African,

and some European co-occurring species, inferences for the other coexisting mysid species may not be robust until gaps in the diet and feeding behaviour are addressed.

Because the feeding habits of mysids exemplify euryphagy and the foregut structure is perhaps influenced mainly by diet rather than phylogeny, it is possible that the gradual transformation of the foregut structure may be governed by the use-induced mechanism proposed recently by Smith and Palmer (1994). These authors noted that growing brachyuran crabs fed with fully shelled molluscan prey developed larger and stronger claws than those raised on nutritionally equivalent unshelled prey. These use-induced changes occurred because the crab exoskeleton and the appendage associated muscle underwent pronounced metamorphosis during molting resulting in a short-term adaptive response to the type of food stimulus. Although there is no evidence that these changes are hereditary, they do point to the fact that , in contrast to the vertebrates, crustacean invertebrates can remodel their feeding appendages based on the type of food being handled throughout growth.

In the case of mysids, different segments of a population inhabiting different environments with different food characteristics would show subtle differences in foregut structure reflecting the diet. Prolonged exposure of this particular sub-population may eventually result in feeding morphology novelty and incipient species. This might have happened in the genus *Mysis* inasmuch as the two representative species examined here have very contrasting diets. *M. mixta* is highly carnivorous whereas *M. stenolepis* is more detritivorous/herbivorous despite both having similar foregut type. These two species have separate north Atlantic sector distribution in that *M. stenolepis* is found in the northern neritic waters of North America while *M. mixta* is more confined in eastern Europe estuaries (Mauchline 1980; Väinöla 1992). Allozyme electrophoresis showed that the two are strongly divergent with *M. stenolepis* giving rise to the other daughter species of the genus (Väinöla 1992). In the present study, the two are separated partly by the number of the cardiac dorsolateral teeth (CDLT) with *M. stenolepis* having fewer (2+2 dentition formula or df) than *M. mixta* (2+3 df).

Miniaturization which involves reduction and structural simplification (Hanken

and Wake 1993) may have been a factor in the foregut evolution in mysids. This process may govern the present foregut features of the two *Anisomysis* species. These species are relatively small in size and show a reduced number of spines in the cardiac chamber. This mechanism may perhaps even be the pathway towards the transformation from a spheroidal to a tubular foregut and the associated macrophagous to suction feeding mode. Miniaturization is usually achieved by developmental heterochrony, in particular paedomorphosis (Futuyma 1986; Barnes *et al.* 1988; Hanken and Wake 1993).

In contrast, adaptation to diet may still be a strong influencing factor because reduction in size does not necessarily accompany the simplification of structures and the reduction in the number of armatures as can be seen in the relatively large sized genera *Paramesopodopsis* and *Siriella.* Furthermore, reduction in size need not always be associated with simplification in function, *e.g.* dealing with mainly fine particles or by suction feeding as may be deduced from the structure in *Anisomysis* species. For instance, the *Mysidopsis* species are the smallest analyzed in the present study yet they are carnivorous and can cope with chitinous and bulky food. This is made possible mainly because of their strong tooth-like spines on the laterale. These examples which contradict the miniaturization theory, lends support to the adequacy theory of adaptation proposed by Gans (1993) which states that the species is adequately matched to its mode of life.

It was hoped that by looking at coexisting species from other parts of the globe, the different foregut types found in the three Tasmanian species would be repeated. It was also expected that because the foregut structure exhibited by the three species indicated feeding specializations which were interpreted to partially explain their coexistence, similar scenarios would be observed in the other co-existing species. Clearly general statements that mysid species co-occur because they show different foregut types as reasoned in chapter 8 cannot be sustained by the evidence presented here. For example, three of the four co-existing species from South Africa share a similar foregut (type Ia for *Rhophalophthalmus terranatalis*, and the two *Gastrosaccus* species). The only distinct foregut type shown which strongly indicates niche

separation is that of *Mesopodopsis wooldridgei* which possesses a tubular foregut (type II). Other niche axes such as size and feeding behaviour need to be invoked to explain their coexistence.

Furthermore, although the diet of the three coexisting Japanese species is not well established, their foregut morphology suggests similar patterns to those in the three Tasmanian species. This similarity may be explained by ecological equivalence in that the predatory *Siriella longipes* is equivalent to *Paramesopodopsis rufa*, *Nipponomysis lingvura* to *Tenagomysis tasmaniae*, and *Anisomysis ijimai* to its congener *Anisomysis mixta australis*. This seems likely because of habitat similarity with these species occupying the same temperate latitudes, habitat depth and substrate characteristics. Depth, habitat association, and size are equally important resource partitioning dimensions (Schoener 1974). The three Tasmanian species have been shown to conform to the Hutchinsonian ratio (Fenton 1986), and all three have been observed to occupy different but adjacent microhabitats in the field (Fenton 1992). Branch (1984) noted that although the co-occurrence of species which are ecologically similar and belong to the same guild is prevalent, the number of species that show specialization of feeding adaptations increases with the number of coexisting species. The origin of these close associations and therefore coexistence may include local speciation; *e.g.*, through wider geographic immigration of those species which are eurytopic or generalized feeders and which easily adapt to conditions in recently colonized habitats (Branch 1984).

The present study takes the approach of a detailed comparison of only one component of each mysid, *i.e.* the foregut, thus caution should be exercised in using this to derive insights on mysid feeding trends. One should be fully aware of the interdependence and cooperation of the other components of the mysid structure and, of course the overall behaviour of the organism (Kinsey and Hopkins 1994). Inferring feeding strategies from phylogenetic trees/relationships created out of foregut internal anatomy should be combined with the network of integrated processes of physiology and biomechanics of the whole organism. No information is available supporting the possibility of the foregut or any feeding structures being strongly

correlated with, say, chemoreceptors and other structures of the whole animal which may be important in the type of food acquisition.

CHAPTER 10

GENERAL DISCUSSION

An ecological community is a collection of populations of species living closely enough for the potential of interaction (Krebs 1985). How these populations interact, if they do, and the possible short and long term consequences of such interactions, are questions which have been repeatedly asked in an effort to explain mechanisms of structuring of communities (May 1984). Competition among species for a limiting resource is an example of these community-organizing interactions. The concept of ecological niche may be used as a theoretical framework when ecologists deal with competition. However, the niche of a species is dynamic and multi-dimensional which make analysis extremely difficult, if not impossible. Three of its dimensions, *i.e.* the utilization of resource such as food, space, and time are often analysed because species are likely to compete against each other in these dimensions (Schoener 1974; Pianka 1994). If competition does occur mechanisms of niche partitioning or segregation are usually invoked to explain co-occurrence of species (Schoener 1974; Pianka 1994).

In this thesis feeding behaviour and comparative morphology of feeding structures are used to shed light on mechanisms of food resource partitioning in shallow water mysids. Although these approaches can be broadly categorized into the two inter-related aspects of structure and function, the subject of behavioural ecology and functional morphology are multi-faceted. It is in the detailed analysis of these facets (autecology) that finer points about the feeding biology of a species may be fully discerned.

The three mysid species, *Anisomysis mixta australis*, *Paramesopodopsis rufa*, and *Tenagomysis tasmaniae*, show a persistent pattern of close coexistence over short (diel) and long (seasonal) temporal scales, but peaks of their abundance are temporally separate (Fenton 1992). Similar patterns were observed in my study site which is a few kilometres north of Fenton's. Intensive breeding of the three mysid species occurs from spring to the end of autumn, with a winter depression in the two

larger species, *P. rufa* and *T. tasmaniae*, and a winter cessation in *A. mixta australis* (Fenton 1994).

Results from a detailed investigation of the different components of feeding behaviour in the present study confirm Fenton's (1986) conclusions from dietary (stomach contents and stable isotope) analyses. For instance, the optimal chemoreception study established a sharper gustatory response of *P. rufa* to betaine-HCl and glycine than the other two species. Acuteness to these dissolved food signals suggests greater sensitivity to fresh and decomposing animal tissue in *P. rufa*. These slight differences, in conjunction with other factors could contribute to feeding niche partitioning.

Although the fine particle capturing mechanisms are similar in the three species the smallest species, *A. mixta australis*, ingested mainly the smallest inert beads, and the other two larger species ingested the full range of sizes from 10 to 90 μm. These results support Wilson's (1975) speculation that larger species feed on a greater range of resources than smaller ones, rather than specializing on larger food items. Results obtained using inert beads indicate that the three mysid species are passive fine particles suspension feeders, and that their utilization of this type of food resource is a function of mysid size. However, the artificiality of the inert beads fed to the three mysid species may have strongly influenced these results. Mysids, like other suspension feeders (Greene 1985; DeMott 1989; Paffenhøffer 1988; Vanderploeg 1990), are capable of active selection based on the quality and quantity of fine food particles.

In the capture of large particles (predatory feeding), *P. rufa* was the most efficient predator on the oblate spheroidal daphniid, *Daphniopsis australis*. The slender and cylindrical prey, *Artemia* sp. metanauplii, was preyed upon by the three species at comparable rates suggesting that the efficiency of the capturing mechanism for this prey is similar in all three species. Shape of these two slow swimming prey types seems to be an important factor in determining their vulnerability to predatory mysids. Fast swimming and elaborate evasive techniques are probably responsible for the negative selection of the copepod prey *Gladioferens*

pectinatus. The three mysid species' prey selectivity, and therefore partitioning of the animal food has been studied by analyzing in detail their prey capturing and ingestion mechanisms. However, this is merely a scratch on the surface of the highly complex and yet to be fully understood mysid-prey interaction. The other components of Holling's predation framework, *e.g.* prey encounter and pursuit, need to be investigated in future studies. Another possible avenue for future research is the multifactorial approach comprising factors such as temperature and salinity, varying densities of the naturally gregarious mysids, prey types, and the effect of these factors on mysid functional responses.

The *in situ* feeding experiments revealed a preference for the *Artemia* sp. nauplii by the three species. By contrast ingestion of algal detritus and phytoplankton was uniformly low. These results suggest considerable but not necessarily total dietary overlap (Schoener 1989).

The investigation of an aspect of the enzymatic digestive phase also provided insights into the mechanism of food partitioning in the three mysid species. Long term variation of the enzyme laminarinase activity (ELA) of freshly caught mysids differed markedly between *T. tasmaniae* and *P. rufa*. The ELA of *A. mixta australis* was similar to that in *T. tasmaniae*, but its reduced level during winter may be either related to its overwintering behaviour, or the reduced level of small laminarin-producing particulate substrate. In general, the level of herbivorousness in these mysids varies in the order *T. tasmaniae* > *A. mixta australis* > *P. rufa*. Time and financial constraints did not permit the investigation of another technique of indirectly assessing food partitioning. This technique involves the determination of respiration and nitrogen excretion rates. The ratio of the respired oxygen to total nitrogen (organic and inorganic) excretion may be related to the feeding habits of zooplankton (Mayzaud 1986). This method may then be complemented with information on glutamate dehydrogenase (GDH) and electron transport system (ETS) activities, both of which give quite accurate estimates of ammonia and oxygen metabolism, respectively (Mayzaud 1986).

The comparable growth rates of the three species on *Artemia* sp. nauplii again suggest overlapping diets. Clutter (1967) speculated that if similar growth is observed in mysids held together in the same experimental conditions it is highly likely that they compete in the field for the same resource. Unlike the other two species, *T. tasmaniae* survived and grew on a diet of algal detritus, and on the diatom, *Phaeodactylum* sp. suggesting a broader feeding niche.

The specializations in the three mysid species' feeding structures further corroborate Fenton's (1986) findings. Feeding adaptations deduced from the subtle morphological specializations suggest food resource partitioning between the three species. For example, the mouthparts and foregut of *A. mixta australis* are best adapted to cope with fine particulate matter and smaller animal prey while those in the other two species are more efficient at dealing with larger and bulky food materials. Complex and primarily for cutting armatures allow *T. tasmaniae* to efficiently feed on tough plant material while simple and mainly for squeezing appendages are the specialized features of the mainly predatory *P. rufa*.

Furthermore, the three species separate along two more ecological niche axes in that they differ in size (conforming to the Hutchinsonian ratio (Fenton 1986)), and microhabitat utilization (Fenton 1986; O'Brien 1987) with *P. rufa* and *A. mixta australis* spending more time aggregated in the water column while *T. tasmaniae* is found on, or a few centimetres above, the sandy substrate.

Three parallel examples of niche partitioning in oceanic zooplankton and/or micronekton are worth mentioning. Firstly, two chaetognath species found in the Southern Benguela current exhibit persistent association and both form a guild with the co-occurring krill *Euphausia lucens* (Gibbons 1994). Competition occurs between chaetognaths during periods of prolonged quiescence and mismatch, but because they have evolved resource partitioning mechanisms for three niche axes: *viz.* depth (vertical space), time of maximal feeding, and size of the exclusive copepod prey, competition is mitigated. Competition with the other guild member (the krill) on similar sizes of the copepod prey is alleviated by a non-historical (unevolved) partitioning, *i.e.* by differential feeding mechanisms. Secondly, Kinsey

and Hopkins (1994) noted that the differences in niche parameters (prey size and day and night distribution) of 27 euphausid species were greatest among species with a specialized morphology, and least among species that were morphologically generalized. They reasoned that resources are partitioned to reduce competition between species, thereby maintaining the high species diversity, but the absence of separation among *Euphausia* species suggests that diversity of these herbivorous and/or omnivorous (lower trophic level) species in the epipelagic zone may be predation controlled as has been hypothesized among oceanic copepods (Poulet 1978; McGowan 1979, 1985). Thirdly, Flock and Hopkins (1993) invoked ecological accommodation by resource partitioning as a mechanism which minimizes competition between eighteen sergestid species, but they also noted that heavy predation crops the populations to the level where sufficient food is available for survivors.

According to Schoener (1974) differences observed in feeding morphology may provide strong evidence of competition as a driving force, not in the present sense, but in the past historical, evolutionary sense. The fact that subtle morphological specializations were found in the three mysid species suggests that the food resource partitioning mechanism is historical or evolved (Gibbons 1994). Immigration and further specialization (by morphological/phenotypic change) could not be ruled out as another important mechanism (Branch 1994). Futuyma (1986) claimed that species coexist because they had already evolved different diets before they encountered each other. *A. mixta australis* has a wide distribution (Fenton 1986), and by virtue of it being eurytopic, it might have immigrated into the coastal waters of Tasmania and invaded the available niche unoccupied by the other two endemic species. As far as the knowledge on their biogeographical distribution is concerned, *T. tasmaniae* and *P. rufa* are restricted to the south-western Pacific region (Fenton 1986), thus the widening of their niches might have evolved over some time. Assuming that their shared gut structures are not homoplastic (structures formed by convergent or parallel evolution), these two species might have shared a more recent common ancestral stock. Enzyme and/or gene electrophoresis might provide

evidence on genetic relatedness and time of divergence between these species. (*e.g.* Väinölä 1992 in *Mysis* spp.). Fenton (1986) also noted that predation pressure might explain the patterns of spatio-temporal distribution of the three mysid species. However, predation may not be very severe because she found only a few fish to be important predators, and of the three species, only *T. tasmaniae* was found to be heavily eaten.

Because living organisms share a common ancestor, ancestral features may place constraints on the functioning of the descendants (Harvey and Pagel 1991). The evolution of structures is often irreversible and some of the elements of a previous structure are no longer available to recreate it because they have been redirected into new essential functions (Stearns 1994). A survey of the foregut features of 48 mysid species revealed shared ancestral features. The primary features of the cardiac region (pre-anteromedianum, laterale, anteromedianum, primary filter), and the pyloric region (inferolaterale, superolaterale, inferomedianum, the secondary filter, and funnel) suggest that the 48 species examined are monophyletic. The constant gross features might be related with a uniform benthopelagic environment where micronektonic mysids are adapted to almost uniform food resource (seston). In this case, selection favors little variation among individuals in feeding ecology and associated morphology by acting strongly against individuals that depart widely from the average phenotype (Grant 1971). In general, however, feeding adaptation appeared to be more important than phylogeny in shaping these structures because of the adequate matching of the other foregut structures directly involved in the processing of food items. These results suggest that the need to collect food items seems to have been such a strong selective force that adaptations of the feeding apparatus have masked phylogenetic relationships within these structures in mysids.

The present study essentially attempted to present points of compatibility between ecology, behaviour and phylogeny, three major biological disciplines which until recently have been thought to be irreconcilable (Harvey and Pagel 1991; Brooks and McClennan 1991). I believe that when these various approaches are

combined comparative biological studies are more rigorously tested and the integrative picture is closer to what is happening in nature.

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APPENDIX 1

MYSID GRAZING RATES DATA

Legend: AP - food combination algal detritus and phytoplankton
AZ - food combination algal detritus and zooplankton
C - grazing chamber
GM - geometric mean of initial (i) and final (f) sub-sample dpm
Σ - total
dpm/ml - GM/volume of sub-sample
(dpm/ml)(h) - dpm/ml x duration of experiment (0.33 h)

Species pair: AP - *A mixta australis, P rufa*
AT - *A mixta australis, T. tasmaniae*
PT - *P rufa, T. tasmaniae*

Date: November 23, 1992

Species: *Paramesopodopsis rufa*

Isotope	Sub-sample		Sub-sample dpm	C	Mysid Biomass (B) (mg DW)	Mysid dpm	GM Sub-sample dpm	Mysid dpm/B	Σ Mysid dpm/B	(dpm/ml)	(dpm/ml)(h)	Grazing Rate ml/(mysid mgDW)/h	Corrected Grazing Rate ml/(mysid mgDW)/h
14C	AP1	i	16057.37	C1	31.94	10031 51	14920 05	0314.12	5607 07	596 80	196.94	28.47	
		f	13863.28		23 05	28720 62		1246 12					
	AZ2	i	10843 94		27.67	58776 89	11696 88	2124 24					
		f	12616 90		21 33	41017.94		1922.58					
	AZ3	i	48446.21	C2	03 92	01653 63	14848 56	0422.23	0529 75	457.88	154 40	03.43	
		f	04551 02		26 88	01253.61		0046 64					
					36 76	00962.55		0026 19					
					28 82	00999 50		0034 69					
				C3	30 54	12211.15		0399 87	2223 00	593.94	196.00	11.34	
					07 37	04184 15		0567 53					
					11 60	03577.12		0308 42					
					01 18	01116 16		0947 18					
3H	AP1	i	19038.55	C1	31.94	16048.23	10768 96	0502.52	5087.26	430.76	142.15	35.79	
		f	06091.35		23 05	20410 81		0885 58					
	AZ2	i	11524.27		27 67	31224.04	12091 06	1128 46					
		f	12685 72		21.33	54845 35		2570.70					
	AZ3	i	35012.41	C2	03 92	03103 09	12888 38	0792 33	0860 49	483 64	159.60	05 39	3.53
		f	04744 33		26 88	00782.47		0029 11					
					36 76	00648.39		0017 64					
					28 82	00616 88		0021.41					
				C3	30.54	08546.41		0279 87	1948.04	515 54	170.13	11 45	9 59
					07 37	06901.10		0936 06					
					11.60	02194 47		0189 21					
					01.18	00639.76		0542 91					

Species: *Tenagomys tasmaniae*

14C	AP1	i	03181.71	C1	07.03	00597.78	07118 80	0085 07	0316.90	0284.75	093.97	003 37	
		f	15927.71		14 30	00822.87		0057.54					
	AZ2	i	52819.54		09 92	00716.15	02758 57	0072.22					
		f	00144.07		05.64	00575.44		0102.07					
	AZ3	i	25897.46	C2	02.74	01624 56	35355.28	0592.82	2725 85	0110.34	036.41	chamber	
		f	48267.12		03.49	00646 57		0185 29				opened	
					08.44	04019 55		0476 19					
					09 33	13731.32		1471.55					
				C3	15.46	01304.28		0084 34	0423.36	1414.21	466 69	000.91	
					21 85	01749 42		0080.07					
					15.11	01759.23		0116 46					
					07.95	01133.05		0142.49					
3H	AP1	i	03023 00	C1	07.03	00879.21	06494.14	0125.12	0453 54	0259.77	085.72	005.29	
		f	13950.99		14.30	01287.21		0090 01					
	AZ2	i	56503.58		09.92	00980 79	02399.29	0098.90					
		f	00101.88		05.64	00786.54		0139.52					
	AZ3	i	21868 65	C2	02.74	01935.22	29582 05	0706 18	3909.67	0095 97	031.67	123 45	122.52
		f	40016.07		03.49	00694.86		0199 12					
					08.44	04569 61		0541.36					
					09.33	22982.79		2463 01					
				C3	15.46	02254.76		0145 81	0783 33	1183.28	390.48	002.01	001.08
					21.85	04228.47		0193.54					
					15.11	03573.62		0236 58					
					07.95	01649 29		0207.41					

Date March 11, 1993

Species: *Tenagomysis tasmaniae*

Isotope	Sub-sample		Sub-sample dpm	C	Mysid Biomass (B) (mg DW)	Mysid dpm	GM Sub-sample dpm	Mysid dpm/B	Σ Mysid dpm/B	(dpm/ml)	(dpm/ml)(h)	Grazing Rate ml/(mysid mgDW)/h	Corrected Grazing Rate ml/(mysid mgDW)/h
14C	AP1	i	22589.22	C1	07 36	0080 43	16520 35	010 92	217 50	826.02	272.59	00 80	
		f	12081 96		10 52	0160 62		015 27					
	AZ2	i	05515 49		05 69	0246 83	03423 69	043 37					
		f	02125.22		10 45	0196.20		018 78					
					05 80	0085 94		014 81	764 87	171.18	056 49	13 54	
					05 34	0224 61		042.09					
					10 47	0472.85		045 18					
					07.20	0111.53		015 48					
					11 44	0132.65		011.59					
				C2	03 03	1352 65		446 77					
					06 56	0012 69		001.93					
					01.87	0591 87		316 17					
3H	AP1	i	03497.95	C1	07.36	0010 67	02848 59	001 45	009.50	142.43	047.00	00.20	
		f	02319.78		10 52			000 00					
	AZ2	i	01841 03		05 69	0006 65	01401.98	001.17					
		f	01067 64		10 45	0003 67		000 35					
					05 80	0021.65		003 73	148 86	070.10	023.13	06 44	5 50
					05 34			000 00					
					10 47			000 00					
					07.20	0020.20		002 80					
					11 44			000.00					
				C2	03 03	0199.31		065 83					
					06 56	0009 96		001 52					
					01.87	0152.59		081.51					

Species: *Anisomysis mixta australis*

14C	AP1	i	6321.58	C1	03 59	0005 03	7782.10	001 40	198 80	389 11	128 40	01.55	
		f	9580 06		03 64	0156 48		043 00					
	AZ2	i	4131.24		02.74	0423.25	2630 61	154 40					
		f	1675.07	C2	12.70	0161.20		012.69					
					17.00	0371 07		021 83	460 58	131 53	043.41	10 61	
					17.85	0094.59		005 30					
					10 21	0414 69		040 60					
					09 83	0099 95		010 17					
					07 54	0055 38		007 34					
					03 19	0012 54		003 93					
					07 19	2580 48		358.72					
3H	AP1	i	1103.73	C1	03.59	0023 77	1256.29	006.62	010 59	062.81	020 73	00.51	
		f	1429.94		03 64	0002.76		000 76					
	AZ2	i	1155 46		02.74	0008 81	1024.71	003 21					
		f	0908.76	C2	12.70			000 00					
					17.00			000 00	000 00	051.24	016.91	00.00	
					17 85			000 00					
					10 21			000 00					
					09.83			000 00					
					07.54			000 00					
					03.19			000 00					
					07.19			000.00					

Species: *Paramesopodopsis rufa*

14C	AP1	i	40614.52	C1	13.45	00114.13	19230 96	0008 49	3288.71	961.55	317.31	010.36	
		f	09105 85		70.94	00750 92		0010 59					
	AZ2	i	05089.34		39.41	00892.87	03219 99	0022.66					
		f	02037.26		20 05	00660.90		0032.96					
					19.27	00726.94		0037.72	5737.39	161 00	053 13	107 99	
					13.28	01751.32		0131.84					
					14 31	00604.91		0042.27					
					05.43	15442.64		2842.06					
					35 57	05695 34		0160 12					
				C2	13 94	09121.81		0654.36					
					19 79	04344 31		0219 52					
					13.29	01444 17		0108.68					
					03.05	14491.30		4754 83					
3H	AP1	i	06081.10	C1	13.45	00012.62	03055.75	0000 94	0118.19	152.79	050.42	002.34	
		f	01535.51		70.94								
	AZ2	i	05356 57		39.41		02132 80						
		f	00849.21		20.05	00091.27		0004 55					
					19 27	00042.59		0002.21	0078.68	106.64	035.19	002.24	1.309
					13.28	00195 95		0014.75					
					14 31	00020.47		0001 43					
					05.43	00512.41		0094 30					
					35.57								
				C2	13 94	00189 79		0013 61					
					19 79	00017.14		0000 87					
					13.29	00066.23		0004 98					
					03 05	00180 46		0059.21					

Date	April 5, 1994										Grazing Rate
APAPreplicate 1		Sub-	Sub-sample	Mysid Biomass (B)	Mysid	GM Sub-	Mysid	Σ Mysid			ml/(mysid
Species	Isotope	sample	dpm	(mg DW)	dpm	sample dpm	dpm/B	dpm/B	(dpm/ml)	(dpm/ml)(h)	mgDW)/h
Anisomys	14C	AP1 i	289053.92	01.77	0635.71	303640 45	358 67	2026.28	6072.81	2004 03	1.01
mixta australis		f	318963.05	01.88	0821 55		438 09				
				01.81	0374 76		206 69				
				01 92	0549 67		285 93				
				02.29	1686 56		736 90				
Paramesopodopsis				09.25	1914.14		207 00	1308 59			0 65
rufa				10.21	1686 14		165 09				
				10.10	1837 55		181 96				
				11.04	1747.47		158.28				
				09.98	1559 18		156 16				
				09 87	1662.65		168 42				
				10 33	1430 72		138 52				
				09.60	1278 92		133 17				
Anisomys	3H	AP1 i	131165.77	01.77	0093 96	125618 95	053 01	0322.34	2512.38	0829 09	0 39
mixta australis		f	120306.70	01.88	0110 03		058 67				
				01.81	0078 47		043.28				
				01.92	0080 35		041.80				
				02.29	0287.42		125 58				
Paramesopodopsis				09.25	0181 82		019 66	0105.87			0.13
rufa				10.21	0116 22		011.38				
				10.10	0089 20		008 83				
				11.04	0096 86		008 77				
				09.98	0112.03		011.22				
				09.87	0263 18		026.66				
				10.33	0138 79		013 44				
				09 60	0056 70		005.90				
APAPreplicate 2											
Anisomysis	14C	AP2 i	259911.08	01 42	0770 09	271791.95	542 04	4819 92	5435 84	1793 83	2 69
mixta australis		f	284215.92	01.47	0913 42		623 15				
				01.08	0836 79		771.60				
				01.21	1046.12		864 42				
				02.65	1066 15		402 32				
				02 44	2030 71		833.21				
				03.22	0999 32		309 96				
				02.87	1358 34		473.22				
Paramesopodopsis				14.29	2643 50		184 93	1851 45			1 03
rufa				14.26	2532.79		177.66				
				16 89	3054 11		180 78				
				12.44	2591 08		208.29				
				18.40	2815 01		153 00				
				15 14	2618 92		172.93				
				16.54	2941.97		177.84				
				15.18	3982.42		262.28				
				13 59	2298 40		169.10				
				23.78	3915.40		164.64				
Anisomysis	3H	AP2 i	108432.01	01.42	0100 30	106983.53	070 60	0425.70	2139 67	0706 09	0 60
mixta australis		f	105554 40	01.47	0127.69		087.11				
				01.08	0103.31		095.26				
				01.21	0084 35		069 70				
				02.65	0083 30		031.44				
				02.44	0119 47		049 02				
				03.22	0022 55		006 99				
				02.87	0044 69		015 57				
Paramesopodopsis				14.29	0011 86		000 83	0140 20			0.20
rufa				14.26	0116 49		008 17				
				16.89	0112.55		006 66				
				12.44	0183 13		014.72				
				18 40	0097 64		005.31				
				15.14	0146 11		009 65				
				16 54	0042.87		002.59				
				15.18	0399.76		026 33				
				13.59	0728 64		053 61				
				23 78	0293 21		012.33				

ATAPreplicate 1											
Anisomysis	14C	AP1	i	346545 30	1.92	0571.06	334382.73	297.06	2562.59	6687.65	2206 93	1.16
mixta australis			f	322647 02	2 44	0816 82		335 02				
					1 85	0566 40		305 40				
					1.89	0560 35		296 77				
					1 74	0574 22		330 01				
					1 98	0600 27		302.80				
					1 76	0729 14		413 34				
					4 05	1142 58		282.18				
Tenagomysis					4 86	0836 66		172.19	1369 50			0 62
tasmaniae					4 90	0747 07		152.40				
					5 31	0871.65		164 17				
					5 49	0874 29		159.26				
					5 41	0816 83		150 86				
					5 41	0752.81		139 04				
					4 33	0874 08		202.08				
					3 31	0759 72		229 49				
Anisomysis	3H	AP1	i	167159.65	1.92	0178 50	160697.55	092.85	0937.78	3213 95	1060 60	0 88
mixta australis			f	154485.26	2.44	0424 89		174.27				
					1 85	0173 75		093 69				
					1 89	0167 75		088 84				
					1 74	0181 44		104.27				
					1 98	0207 79		104 82				
					1.76	0336 38		190.69				
					4.05	0357.71		088 34				
Tenagomysis					4 86	0472.86		097.32	0756 11			0.71
tasmaniae					4 90	0383.55		078.24				
					5 31	0510 74		096.20				
					5 49	0514 54		093 73				
					5.41	0456 60		084 33				
					5.41	0392.58		072.51				
					4.33	0506 86		117 18				
					3 31	0386 00		116 60				
ATAPreplicate 2												
Anisomysis	14C	AP2	i	337426.55	1 59	2040 28	321223.89	1282.39	8037.86	6424 48	2120 08	3.79
mixta australis			f	305799.26	1.87	1916 57		1024 36				
					1.91	1703 38		0890 52				
					2.26	1533 53		0679.76				
					2.19	1886 10		0859 82				
					3 68	3055 92		0830.19				
					0 79	1961 84		2470 84				
Tenagomysis					7.07	5939 61		0840 07	8088.70			3 82
tasmaniae					7.13	4063 65		0570 10				
					7 43	5616 36		0756 41				
					8.39	8159 16		0972.72				
					8 06	4842.09		0601.13				
					7.62	5941.63		0779.25				
					7.76	4913.39		0633.48				
					7.30	4374 95		0599 37				
					7.82	4591 07		0587.42				
					5.70	9975.42		1748.75				
Anisomysis	3H	AP2	i	93805.31	1.59	0311 54	115712.21	0195 81	1670 52	2314.24	0763 70	2 19
mixta australis			f	142735.15	1.87	0597.23		0319.20				
					1.91	0348.65		0182.27				
					2.26	0355 01		0157.36				
					2.19	0334 36		0152.43				
					3.68	0313 48		0085.16				
					0 79	0459 16		0578.28				
Tenagomysis					7.07	0642.40		0090.86	0968 41			1.27
tasmaniae					7.13	0570 82		0080 08				
					7.43	1021.64		0137 59				
					8 39	0819.16		0097.66				
					8 06	0716 55		0088 96				
					7 62	0654 21		0085 80				
					7.76	0923 62		0119 08				
					7.30	0628.32		0086 08				
					7.82	0777 96		0099 54				
					5 70	0472.11		0082.76				

PTAPreplicate 1											
Paramesopodopsis	14C	AP1	i	358483.61	10 14	3419 71	359710 93	0337 35	2702.37	7194.22	2374 09	1.14
rufa			f	360942.46	08 82	2499 58		0283 30				
					10 96	3038 36		0277 17				
					11.08	2571 38		0232.03				
					10.21	3365 75		0329 55				
					09.28	2756 29		0296 91				
					09.83	2765 10		0281.18				
					09 86	2553 21		0259.08				
					04 48	1818 44		0405 80				
Tenagomysis					05.04	3011 95		0597.04	4838.71			2 04
tasmaniae					05 40	3680 91		0681 73				
					05 10	3025 90		0592.90				
					04.79	3037 61		0634 42				
					04 99	2879.25		0577 33				
					05 82	3044 31		0523.51				
					05 60	3247.31		0580.21				
					03.35	2185 40		0651 58				
Paramesopodopsis	3H	AP1	i	100022.00	10.14	0423 35	105851.99	0041.76	0380.13	2117.04	0698 62	0 54
rufa			f	112021.80	08 82	0334.95		0037.96				
					10 96	0399 82		0036 47				
					11.08	0412.79		0037.25				
					10.21	0488 93		0047 87				
					09.28	0412 09		0044 39				
					09 83	0747 64		0076 03				
					09 86	0575 44		0058.39				
					04 48	0326 59		0072.88				
Tenagomysis					05 04	0558 81		0110 77	0998.54			1 43
tasmaniae					05.40	0683 82		0126 65				
					05.10	0657 03		0128 74				
					04.79	0592.80		0123.81				
					04.99	0616 90		0123 70				
					05 82	0552.51		0095.01				
					05.60	0631.85		0112.90				
					03 35	0593 57		0176 97				
PTAPreplicate 2												
Paramesopodopsis	14C	AP2	i	298016.18	15 10	3671 53	251526 59	243 08	2931.69	5030 53	1660.08	1.77
rufa			f	212289.23	11.87	2881 93		242.89				
					12 47	3854.88		309.04				
					12 33	3073 59		249.29				
					12.44	3194 63		256 85				
					15 68	3071 03		195 80				
					13.55	3628 93		267.78				
					12.69	3808 65		300 08				
					12.22	2945 40		241.00				
					13 02	2730 19		209 61				
					13.67	2561.68		187.41				
					11.34	2594 42		228 86				
Tenagomysis					07 92	2975 69		375.72	4028.12			2.43
tasmaniae					07.40	3828.76		517.73				
					07 40	3355 77		453.77				
					07.69	3102.20		403.29				
					07.77	2984 09		383.93				
					07 89	3287 08		416 65				
					08.17	1291.86		158.05				
					07.74	3247.78		419.51				
					07.37	3440 48		467.04				
					09.11	3939 45		432.43				
Paramesopodopsis	3H	AP2	i	136226.09	15 10	0794 07	135336 37	052.57	0841 44	2706.73	0893.22	0 94
rufa			f	134452.47	11.87	0525 30		044.27				
					12.47	1287.50		103.22				
					12.33	1546 73		125.45				
					12.44	0617.64		049 66				
					15 68	1317 93		084 03				
					13.55	0763 41		056 33				
					12 69	0818 10		064.46				
					12.22	0567.72		046.45				
					13.02	1373 66		105.47				
					13 67	0760 02		055 60				
					11 34	0611 45		053.94				
Tenagomysis					07.92	1061.81		134 07	1454.08			1.63
tasmaniae					07 40	1479.14		200 01				
					07.40	0862.51		116 63				
					07 69	1307 60		169 99				
					07 77	1614 16		207 68				
					07.89	1140 38		144 55				
					08.17	0437 22		053 49				
					07.74	1182.46		152.74				
					07.37	1167.23		158 45				
					09.11	1061 13		116 48				

Date	April 5, 1994											Corrected
APAZreplicate 1											Grazing Rate	Grazing Rate
		Sub-	Sub-sample	Mysid Biomass (B)	Mysid	GM Sub-	Mysid	Σ Mysid			ml/(mysid	ml/(mysid
Species	Isotope	sample	dpm	(mg DW)	dpm	sample dpm	dpm/B	dpm/B	(dpm/ml)	(dpm/ml)(h)	mgDW)/h	mgDW)/h
Anisomysis	14C	AZ1 i	31756.81	02.36	089495 06	28834 46	37886 32	099593 08	576.69	190 31	523 33	195 80
mixt australis		f	26181.04	02.10	040484 72		19294 98					
				01.84	035033 57		19062 78					
				03 07	071595 09		23349 02					
Paramesopodopss				09 72	138991.58		14296 02	109733 79				
rufa				12.17	169140 04		13899.71				576 61	215 74
				12.52	169743 39		13561.46					
				14 02	152344 86		10864 70					
				12.30	151250 69		12298 60					
				11 74	227009 83		19333 15					
				08 99	118877 35		13228 00					
				09 00	110208 10		12252.15					
Anisomysis	3H	AZ1 i	28732.02	02.36	004727 89	14449 60	02001 48	007899 64	288 99	095.37	082.83	57.96
mixt australis		f	07266.84	02.10	003502 62		01669.34					
				01 84	003486 45		01897.08					
				03.07	007149 81		02331 74					
Paramesopodopss				09 72	013076 94		01345 03	008794 75				
rufa				12.17	014002.80		01150.73				092 22	64.82
				12.52	010499 67		00838 86					
				14 02	022868 74		01630 92					
				12.30	011425 67		00929 05					
				11 74	015136 86		01289 12					
				08 99	007142 15		00794.74					
				09 00	007342.55		00816.29					
APAZreplicate 2												
Anisomysis	14C	AZ2 i	60451.72	01.42	028574 57	45335.26	20162.70	112098 48	906.71	299.21	374.64	220.38
mixta australis		f	33998 80	01.19	032860.42		27576 72					
				02.25	031177 80		13879 01					
				01.74	043687.66		25107.85					
				01.52	038522 62		25372.21					
				01.97	025031 64		12680 67					
				01 10	023668 44							
Paramesopodopsis				08 96	133682.42		14916.25	145206.72			485 30	285.47
rufa				08.21	162071 30		19741.20					
				10.10	125080 76		12385 95					
				09 10	233299 88		25631 72					
				09 10	166888 69		18331.76					
				10.37	148215 59		14296 31					
				06.19	148293.28		23942.21					
				08 51	135865 96		15961 32					
				13 38	087679.30		06553.45					
Anisomysis	3H	AZ2 i	21869.05	01.42	002085 28	19638.87	01471 41	006217.22	392.78	129 62	47.97	19.98
mixta australis		f	17636.12	01.19	001921 39		01612.44					
				02.25	001843 45		00820 62					
				01.74	002024.10		01163.27					
				01.52	001745.24		01149 47					
				01.97	001874 37		00949.53					
				01.10	001956 95		01771.44					
Paramesopodopsis				08.96	006782.92		00756 84	005266.44			40.63	04.38
rufa				08.21	004348 65		00529 69					
				10.10	003248.02		00321.63					
				09 10	005687 23		00624 83					
				09.10	005793 78		00636 41					
				10 37	007499 59		00723 38					
				06 19	005365 29		00866.24					
				08 51	006872.86		00807.41					
				13.38	003746 39		00280 02					

ATAZreplicate 1												
Anisomysis	14C	AZ1	i	53789.58	1.52	282023 31	37425.29	184981.84	214463 95	748.51	247.01	868 25	421.63
mixta australis			f	26039 47	2 12	040284 82		019031.00					
					6 97	072802 48		010451.12					
Treganomysis					6 07	090040 74		014830 31	103220.50			417 89	202 93
tasmaniae					5 52	077109 56		013966 09					
					5.22	074062.33		014188 19					
					5.35	082996 14		015507.50					
					4 39	088617 55		020177.04					
					6 41	072816 57		011352.75					
					5 96	078645 29		013198 62					
Anisomysis	3H	AZ1	i	17305 36	1.52	002566 71	15991 09	001683 53	003016 46	319.82	105.54	028 58	000.00
mixta australis			f	14776.64	2.12	001804 61		000852.52					
					6.97	003346 60		000480 42					
Treganomysis					6 07	002635.80		000434 13	004258 91			040 35	014 58
tasmaniae					5.52	003635 33		000658 43					
					5.22	002830.99		000542.34					
					5 35	004078 43		000762.04					
					4.39	003892 12		000886.18					
					6.41	003517 78		000548.45					
					5 96	002546 29		000427 33					
ATAZreplicate 2													
Anisomysis	14C	AZ2	i	64623.27	02.11	058957 04	49061.04	27978 85	133342.55	981.22	323 80	411.80	262.15
mixta australis			f	37246 43	01.96	053962.76		27579 86					
					02.59	048636 81		18746 84					
					04 14	140400 63		33893 55					
					03.15	079201 87		25143 45					
Tenagomysis					04.26	119142.84		27967 80	167766 38			518 11	329.82
tasmaniae					05 18	097633 07		18855 36					
					04 39	097244 52		22141 89					
					05.02	109732.89		21876.57					
					05 44	076101 05		13977 86					
					04 82	089451 87		18570 81					
					05 19	071116 11		13699 36					
					11.40	349806 75		30676 73					
Anisomysis	3H	AZ2	i	20430.91	02.11	001542.02	17608 67	00731.78	2789 83	352.17	116.22	024 01	000 00
mixta australis			f	15176.29	01.96	001395 66		00713.31					
					02.59	001280 02		00493.38					
					04.14	002244 89		00541 93					
					03 15	000974.72		00309 43					
Tenagomysis					04.26	001115 86		00261 94	4546 54			039.12	000.00
tasmaniae					05.18	002731.63		00527 55					
					04 39	002473 87		00563.28					
					05.02	001941.95		00387 15					
					05 44	002775 65		00509.82					
					04.82	005257.55		01091.50					
					05.19	001030 48		00198.50					
					11 40	011480 54		01006 80					

PTAZreplicate 1												
Paramesopodopsis	14C	AZ1	i	018998 14	14 02	209051.23	52850 43	14908 16	159940 36	1057.01	348 81	458.53	314.44
rufa			f	147023.21	12.74	228346 99		17927.28					
					10 33	250439 54		24253 30					
					10 67	239352.78		22423 91					
					12.74	196866 09		15455 02					
					14 02	159495 43		11374 66					
					13 88	535781.70		38598.21					
					11 49	172281 94		14999 82					
Tenagomysis					05 86	090033 62		15355 71	158808 94			455.28	312.21
tasmaniae					06 83	111915 92		16397 94					
					05 19	113241 43		21814 11					
					05 57	093506 95		16795 44					
					05.91	121868.58		20618 65					
					05 83	090928 65		15594 54					
					04 82	084348 59		17511 33					
					04 14	062785 90		15152.50					
					04 75	092873 11		19568 71					
Paramesopodopsis	3H	AZ1	i	005262.97	14 02	018487 99	16563 93	01318 44	006594 73	0331.28	109.32	060 32	020.39
rufa			f	052131.00	12.74	010510 04		00825 13					
					10 33	018881 40		01828 53					
					10.67	007059 89		00661.41					
					12.74	007631.80		00599 14					
					14 02	006370.19		00454 30					
					13 88	004782.90		00344 56					
					11 49	006468 85		00563.21					
Tenagomysis					05 86	004445 46		00758.20	006081.62			055 63	015.98
tasmaniae					06 83	002024 17		00296 58					
					05 19	005544 46		01068 05					
					05 57	003648 19		00655.28					
					05.91	005237 63		00886 14					
					05 83	003177 87		00545.01					
					04 82	002560 45		00531.57					
					04 14	002745 30		00662 54					
					04.75	003218 97		00678.25					
PTAZreplicate 2													
Paramesopodopsis	14C	AZ2	i	70199 90	12.65	125489 52	50603 39	09921 69	52417.37	1012.07	333.98	156.95	103.05
rufa			f	36477.31	12.52	074535 95		05955.25					
					10.96	071038 70		06480 45					
					10 41	077863 85		07482.30					
					11.74	077165 24		06571 73					
					10.29	055277 95		05371 69					
					09 36	059208 13		06328 90					
					15.68	067528 52		04305 35					
Tenagomysis					04.89	039448 93		08072.22	75418.02			225.81	148 27
tasmaniae					05.21	047404 16		09106 38					
					05.31	062695 19		11808.34					
					05.24	051392.34		09815 94					
					05.22	064331.72		12324 65					
					05 96	065219 57		10945 45					
					04 76	063527.72		13345 04					
Paramesopodopsis	3H	AZ2	I	26233.61	12.65	002635 93	21400 40	00208 41	02581.97	0428 01	141.24	018 28	005.19
rufa			f	17457.65	12.52	002669.65		00213 30					
					10 96	003162.05		00288 46					
					10.41	003110 53		00298.91					
					11.74	007825 28		00666 43					
					10.29	002803 98		00272.48					
					09.36	000609 39		00065.14					
					15 68	008922.35		00568 85					
Tenagomysis					04 89	000566 07		00115.83	01264.83			008.96	000.00
tasmaniae					05.21	000576 86		00110 82					
					05 31			00000.00					
					05.24	000375 41		00071.70					
					05.22	001352.08		00259 03					
					05.96	000543 42		00091.20					
					04.76	002933 61		00616.25					

APAPreplicate 1			July 29,1994									Grazing Rate	Corrected
		Sub-	Sub-sample	Mysid Biomass (B)	Mysid	GM Sub-	Mysid	Σ Mysid				ml/(mysid	Grazing Rate
Species	Isotope	sample	dpm	(mg DW)	dpm	sample dpm	dpm/B	dpm/B	(dpm/ml)	(dpm/ml)(h)		mgDW)/h	ml/(mysid mgDW)/h
Anisomysis	14C	AP	i	09775 47	04 97	075.04	14289 49	15.11	50 11	408.27	134 73	0.37	
mixta australis			f	20887.94	06 46	049 83		07 71					
					05 84	099 16		16 99					
					04 97	051.14		10.29					
Paramesopodopsis					16.63	306 82		18.45	84 88			0 63	
rufa					17 58	506 80		28.83					
					19 91	143 64		07 21					
					20 37	619 09		30 39					
Anisomysis	3H	AP	i	04846.05	04 97	074 09	04919.31	14.92	54.79	140.55	046.38	1 18	
mixta australis			f	04993.68	06 46	060.34		09.34					
					05 84	077 83		13 34					
					04 97	085 40		17.18					
Paramesopodopsis					16 63	174 72		10 51	33.21			0 72	
rufa					17.58	098 65		05.61					
					19 91	203 82		10 24					
					20 37	139.60		06 85					
APAPreplicate 2													
Anisomysis	14C	AP	i	15581.85	05 45		15581.85		01.77	445.20	146 91	0 01	
mixta australis			f	15581.85	05 70	005.26		00.92					
					05 42	002 79		00.51					
					04.97	001.68		00.34					
Paramesopodopsis					19.23	007 06		00 37	17 02			0 12	
rufa					17.86	033.20		01.86					
					16 86	098 01		05 81					
					19.28	173.27		08.99					
Anisomysis	3H	AP	i	03465 88	05 45	050 99	03465 88	09 36	42.12	099 03	032.68	1.29	
mixta australis			f	03465 88	05.70	052.70		09.25					
					05 42	081 48		15.02					
					04.97	042.18		08 49					
Paramesopodopsis					19.23	111.24		05 78	37.37			1.14	
rufa					17.86	213 08		11 93					
					16 86	156.23		09.27					
					19.28	200.25		10.38					
APTAZreplicate 1													
Anisomysis	14C	AZ	i	0176 61	05.97	00764 68	0751.67	0128.02	0547.60	21.48	07 09	077.27	
mixta australis			f	3199.19	05 54	00677.93		0122.35					
					07.94	02359 93		0297.22					
Paramesopodopsis					20 70	04140 97		0200 05	1144.77			161.53	
rufa					17.22	03333 99		0193 61					
					17.74	04669 59		0263.22					
					18 16	03550.62		0195.52					
					08 45	02470 50		0292.37					
Tenagomysis					08.71	10491 83		1204.57	2367.46			334 05	
tasmaniae					13.37	15547 84		1162.89					
Anisomysis	3H	AZ	i	0374.08	05.97	00530.23	1188 31	0088.77	0330 61	33 95	11.20	029.51	29.07
mixta australis			f	3774.82	05 54	00540 68		0097.58					
					07.94	01145 44		0144 26					
Paramesopodopsis					20 70	00920.72		0044 48	0275.84			024 62	23.64
rufa					17.22	00953 99		0055.40					
					17.74	00598 90		0033.76					
					18 16	01036.18		0057.06					
					08.45	00719 43		0085 14					
Tenagomysis					08.71	01233 72		0141 64	0212.77			018 99	16.97
tasmaniae					13.37	00951 00		0071.13					

APAZreplicate 2												
Anisomysis	14C	AZ	i	8669 60	04 97	1029 63	8153 88	207 38	844.23	232.97	76 88	10 98	
mixta australis			f	7668.83	05 45	1290 85		237.07					
					05 97	1221 79		204 66					
					06 70	1306 59		195 13					
Paramesopodopsis					17 46	3821 64		218.88	668.96			08 70	
rufa					18.97	3805.74		200 62					
					18.71	2344 87		125.33					
					31 78	3944 40		124.13					
Anisomysis	3H	AZ	i	3977 47	04 97	0366 03	4609.49	073.72	176 33	131.70	43 46	04.06	3.34
mixta australis			f	5341.94	05 45	0270 32		049.65					
					05.97	0222.18		037.22					
					06 70	0105 46		015.75					
Paramesopodopsis					17.46	0343.21		019.66	065 41			01.51	0.94
rufa					18.97	0082.44		004.35					
					18 71	0665 22		035.55					
					31.78	0186 04		005 85					
APAZreplicate 3													
Anisomysis	14C	AZ	i	6133 45	06 37	0864 36	6133 45	135 74	661.51	175.24	57.83	11.44	
mixta australis			f	6133 45	05 45	0737.97		135.53					
					04 86	0893 70		183 89					
					02 90	0599 27		206 36					
Paramesopodopsis					18 97	3357 93		177.01	739 88			12 79	
rufa					21.48	2582.68		120.24					
					25 06	3255 95		129.93					
					22.29	6970 17		312.70					
Anisomysis	3H	AZ	i	4936.55	06 37	0060.21	4936 55	009.46	022.15	141.04	46 54	00 48	0.00
mixta australis			f	4936 55	05.45								
					04 86	0024.90		005 12					
					02 90	0021.97		007.57					
Paramesopodopsis					18 97	0236.37		012.46	047.48			01.02	0.39
rufa					21.48	0237.23		011.04					
					25 06	0133 96		005.35					
					22.29	0415 32		018 63					

APPENDIX 2

ARTEMIA SP. GRAZING ON ALGAL DETRITUS

The grazing rates of algal detritus by *Artemia* sp. metanauplii were determined in a laboratory experiment. Both grazer and food were obtained from the preparations in the *in situ* feeding behaviour study (chapter 5). Fifteen metanauplii were pipetted into a 500-mL glass jar containing 0.45 μm Millipore-filtered seawater. In order to measure adsorption levels of ^{3}H-Thymidine by the metanauplii, fifteen cold-narcotized and heat-killed metanauplii were used for the control. The concentration of algal detritus suspension added into each jar was similar to those in the *in situ* experiments. An experimental jar was replicated three times. The control was ran concurrently with the replicate jars. Immediately after adding algal detritus to the experimental and control jars, 5 mL was withdrawn from each jar using a sterile syringe for the initial determination of algal detritus radioactivity. Samples were filtered through 0.45 μm (pore size) HA Millipore filters (2.5 cm diameter). Filters were placed on glass scintillation vials and stored in ice-filled eski container. After 18 min incubation, the metanauplii were carefully filtered through a 80 μm nylon mesh, and quickly resuspended in sterile 0.45 μm Millipore filtered seawater. Swimming animals were quickly pipetted out and placed on filters which were in turn placed on scintillation vials and stored with the other vials. Five mL was withdrawn from each jar for the final measurement of algal detritus radioactivity. The determination of sample radioactivity is as described in chapter 5.

The experiment was carried out at 32 ‰ salinity, and at 10 and 15°C water temperatures. Salinity and temperatures are similar to those experienced by the metanauplii in the field experiments.

Table 1 shows the calculation of the grazing rates. The average grazing rates on algal detritus by metanauplii were similar at 10 and 15°C. Averages were pooled in the calculation of the correction factor. Because the biomass of the metanauplii was not determined, ingestion rates of metanauplii by mysids (in terms of the number of prey ingested) were first derived from the uncorrected clearance rates from the *in situ*

experiment. The number of metanauplii from these *in situ* ingestion rates were then multiplied by the average grazing rate of algal detritus by the metanauplii obtained in the present experiment. The grazing rates from this procedure was then used to subtract *in situ* grazing rates of algal detritus by mysids in conditions where mysids were allowed to feed on a mixture of algal detritus and metanauplii.

Table 1 Grazing rates of *Artemia* sp. metanauplii on algal detritus at 10°C and 15°C.

Isotope: 3H Temperature 10°C	Sample	Sample dpm	*Artemia* number	*Artemia* dpm	Geometric mean (i & f) sample dpm	dpm/ *Artemia*	dpm/mL	(dpm/mL)(h)	Grazing Rate ml/ *Artemia*/ h
	10Ainitial (i)	334.52	15	026.52	320 42	01 77	64.08	19.23	0.09
	10Afinal (f)	306.92							
	10Binitial (i)	250.18	15	430 36	206.98	28.69	41.40	12.42	2.31
	10Bfinal (f)	171.24							
	10Cinitial (i)	223.62	15	050 63	185 14	03 38	37.03	11.11	0.30
	10Cfinal (f)	153 28						mean	0.90
								SD	1.22
15°C									
	15Ainitial (i)	194 05	15	150 41	158 51	10.03	31.70	9.51	1.05
	15Afinal (f)	129 47							
	15Binitial (i)	289.95	15	132.56	196.64	8.84	39.33	11.80	0.75
	15Bfinal (f)	133.36							
	15Cinitial (i)	265.87	15	168.52	171.27	11.23	34.25	10.28	1.09
	15Cfinal (f)	110 33						mean	0.97
								SD	0.19

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COMPARATIVE FOREGUT FUNCTIONAL MORPHOLOGY OF THREE CO-OCCURRING MYSIDS (CRUSTACEA: MYSIDACEA) FROM SOUTH-EASTERN TASMANIA

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The foregut of three co-occurring mysid species was examined using scanning electron and light microscopy. Earlier work suggested there was considerable overlap in their diets. Differences observed in the gut volume and the morphology of the internal gut armature of the cardiac region suggest food resource partitioning between the species, and hence help to explain their co-existence.

INTRODUCTION

Studies of mysid diets by gut contents analysis have generally revealed a broadly omnivorous feeding habit, but there are also tendencies towards carnivory, herbivory and/or detritivory (*e.g.* Nath & Pillai, 1973; Siegfried & Kopache, 1980; Mauchline, 1980; Zagursky & Feller, 1985; Wooldridge & Bailey, 1982; Webb & Wooldridge, 1989). Examination of feeding structures is also necessary to support inferences about feeding ecology (*e.g.* Webb & Wooldridge, 1989). However, there have been few studies relating to the functional morphology of mysid foreguts (Gelderd, 1909; Haffer, 1965; Nath & Pillai, 1973; Mauchline, 1980; Friesen *et al.*, 1986; Webb & Wooldridge, 1989; Storch, 1989). With the exception of the latter two studies, qualitative descriptions and characterization of the different internal foregut structures have been primarily based on light microscopy. These studies may misinterpret the internal arrangement, topography, and three-dimensional orientation of the internal armature of the foregut, mainly due to problems with depth of field (Grice & Lawson, 1971). Oshel & Steele (1988), from SEM observations, briefly described some foregut features of *Gnathophausia ingens*. In a comparative study, Storch (1989), using the techniques of transmission and scanning electron microscopy, described in detail the different food chambers and channels, cuticular ridges, and ultrastructure of the epithelial and cuticular linings of the mysid foregut. Webb & Wooldridge (1989) noted the strong relationship between mouthparts, foregut morphology, and the feeding habits of two co-occurring mysids.

Three mysid species, *Paramesopodopsis rufa* Fenton, 1985, *Anisomysis mixta australis* Zimmer, 1918, and *Tenagomysis tasmaniae* Fenton, 1991, occur together in many shallow inshore regions of south-eastern Tasmania (Fenton, 1992). They occupy a similar depth range of 1·2 to 6 m, and a certain degree of microhabitat partitioning has been observed

in the field (Fenton, 1992). In the daytime, *P. rufa* and *A. mixta australis* spend more time aggregated in the water column while *T. tasmaniae* is found on, or a few centimetres above, the sandy substrate. Gut contents analysis showed a marked overlap in their diet, which includes macroalgal tissue, crustacean remains, dinoflagellates, pine spores, and a large proportion of unidentifiable particulate matter (Fenton, 1986). Food resource partitioning as indicated by a predominance of crustacean remains in *P. rufa*, fine particulate materials in the foreguts of *A. mixta australis*, and macroalgal particles in *T. tasmaniae* has been proposed to explain partially their co-occurrence. In the present investigation, we use scanning electron and light microscopy to describe and compare the structure of the foregut internal armature of these mysids, and infer their probable functions.

MATERIALS AND METHODS

Mysid field collection and laboratory maintenance are described by Metillo & Ritz (1993). Adult mysids were cold narcotized before stomachs were carefully removed under a binocular dissecting microscope. Stomachs for SEM and whole animals for serial sectioning were fixed for 2 h in a solution of 2·5% glutaraldehyde, 0·2M phosphate buffer (pH=7·3), and 0·14M NaCl. Fixed specimens were washed three times for 10 min each with phosphate buffer, followed by post-fixation in 2% osmium tetroxide in 1·25% sodium bicarbonate (pH=7·2) for 2 h. Tissues were washed as before, and rinsed with distilled water. Specimens were then dehydrated by placing them in an ascending series of ethanol concentrations (10 min in each).

Specimens for scanning electron microscopy were immersed in 100% hexamethyldisilazane (Sigma Chemical Company) for 10-15 min, and air-dried overnight at room temperature (Nation, 1983). Hexamethyldisilazane has proven to be effective in the highly chitinous foreguts of mysids without the use of critical point drying. Prior to examination, tissues were mounted on aluminium stubs, sputter-coated with gold, and examined at an accelerating voltage of 15 kV in a Philips 501 scanning electron microscope (SEM). For light microscopy, alcohol dehydrated specimens were washed three times for 10 min each in 100% propylene oxide. Tissues were then embedded in epoxy resin. Line drawings were prepared from serial semi-thin (1 μm) sections using a camera lucida. Semi-thin sections were stained with toluidine blue (Storch, 1989).

Foregut capacities may indicate feeding habits as reported in other peracarids (Jones, 1968; Sheader & Evans, 1975), and euphausiids (Nemoto, 1977). To test this hypothesis, we compared the gut capacity of the three mysid species adults using the foregut index (FGI=LCx100/LV, where LC is the length of the cardiac region, and LV the length of the ventral plate from the cardiac region to the pyloric region) used by Suh & Nemoto (1988). In addition, the formula of a prolate spheroid which best approximates the shape of the mysid foregut filled with food, $4/3\pi a^2 b$ (where a is half the average of the stomach width and height, and b is one half the stomach length), was calculated for each dissected foregut to estimate volume (Murtaugh 1984). Mysids used in the FGI and gut

volume calculations had previously been fed with a mixture of finely-ground oven-dried (60°C) macroalgae and powdered fish pellets until their stomachs were full. Total lengths (tip of carapace rostrum to tip of telson) of 15 heat-killed individuals were measured, and their foreguts dissected out to estimate FGI and gut volume.

RESULTS

Gross morphology of the mysid foregut

The general foregut structure is similar in the three species of mysids (Figure 1), thus transverse sections are shown for only one species (Figure 1B). Foregut features in common are described here briefly. Storch (1989) provides detailed coverage. For convenience in the description and homology of structures, the terminology used by Storch (1989) is followed.

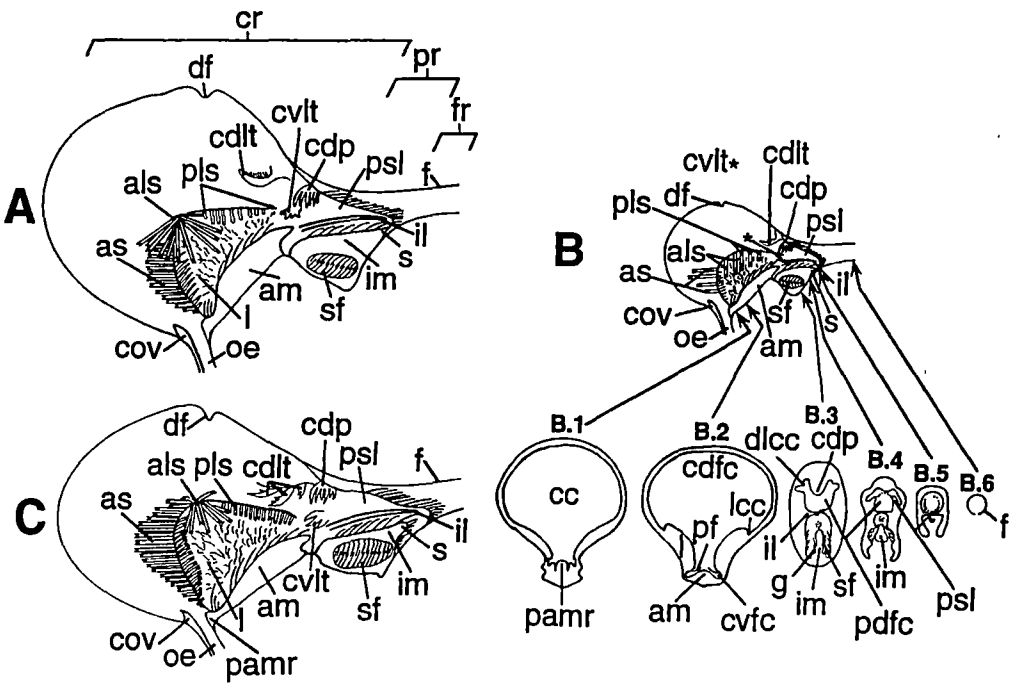

Figure 1. Diagrammatic internal lateral view of right side of the foregut of three mysid species (inferomedianum not in longitudinal section to show the secondary filters). (A) The foregut of *Paramesopodopsis rufa*. (B) The foregut of *Anisomysis mixta australis* with transverse sections (B.1-B.6) of the different regions; arrows indicate the sectioned region. (C) The foregut of *Tenagomysis tasmaniae*. Abbreviations: als, anterolateral spines; am, anteromedianum; as, spines on anterior laterale; cc, cardiac chamber; cdfc, cardiac dorsal food channel; cdlt, cardiac dorsolateral tooth; cdp, cardiac dorsal piece, cov, cardio-oesophageal valve; cr, cardiac region; cvfc, cardiac ventral pyloric channel; cvlt, cardiac ventrolateral tooth; df, dorsal fold; dlcc, dorsolateral circulation channel; f, funnel; fr, funnel region; g, groove of secondary filtration channel, il, inferolaterale; im, inferomedianum; l, laterale; lcc, lateral circulation channel; oe, oesophagus; pamr, pre-anteromedianum ridge; pdfc, pyloric dorsal food channel; pf, primary filter; pls, posterolateral spines; pr, pyloric region, psl, pyloric superolaterale; s, spigot.

The chitinous foregut is divided into anterior cardiac, middle pyloric, and posterior funnel regions. At the junction between the oesophagus and the anterior cardiac region, a cardio-oesophageal valve projects anterodorsally. Behind the valve is the spine-bearing pre-anteromedianum ridge, the lateral margins of which meet the ventral margins of the anterior lateralia. The roof of the cardiac chamber is devoid of any projections, except the prominent dorsal fold. Cuticular ridges armed with spines are situated on the lateral and ventral regions (*e.g.* Figures 1, 2A, 3A & 4A). The bilaterally symmetrical lateralia form the most conspicuous cuticular ridges on the ventrolateral walls of the cardiac region. Each laterale is thickest at its anterior region, and rows of spines line the margin of this region. On the ventromedial margin of the laterale a row of widely-spaced and medially-projecting, barbed spines may be present. Underneath these spines is a row of closely-spaced, bristled spines, the primary filter, which separates the cardiac chamber into narrow ventral and wider dorsal food channels. The tips of the primary filter spines touch the side of the most prominent ventral ridge, the anteromedianum, on the dorsal surface from which arise spines which curve posteriorly. The anteromedianum terminates at the junction between the cardiac and pyloric regions as a tongue-like structure. Grooves on the sides of the lateralia form the lateral circulation channels (these become dorsolateral in the pyloric region). The dorsolateral and ventrolateral teeth are located in the posterior cardiac region, at the cardio-pyloric junction. The ventrolateral teeth, which project into the lumen of the pyloric dorsal food channel, appear to dovetail each other. Dorsal to the cardiac ventrolateral teeth, and slightly behind the cardiac dorsolateral teeth, is the unpaired cardiac dorsal piece which comprises various spines.

The pyloric region bears prominent ventrolateral ridges, called the inferolateralia, which are a continuation of the ridge where the primary filter projects. The inferolateralia divide the pyloric region into a dorsal food channel, and a ventral filtration channel which communicates with the cardiac ventral filtration channels. The pyloric ventral filtration channel is separated by a prominent ventral ridge, the inferomedianum. The apex of this ridge is set out with a row of bristled spines. The inferomedianum ends posteriorly as a slender spigot. Dorsal to the inferolaterale is the pyloric superolaterale fringed by a single row of bristled spines. The walls facing the inferomedianum also bear rows of dorsomedially-projecting spines. On the sides of, and running along the length of, the inferomedianum are two pairs of secondary filtration channels bounded at the sides by secondary filters.

Coarse and undigested food particles are carried into the funnel region, a thin, spine-free tube which joins the anterior region of the long midgut.

Foregut features in the three mysid species

Paramesopodopsis rufa

The foregut of *P. rufa* has the largest length-specific volume of the three mysid species, but its FGI is not significantly different from the other two (Table 1). This large gut capacity is attributed to the spacious cavity formed by the anterodorsal region of the cardiac stomach. At the dorsal margin of the anterior laterale, four distinct rows of

spines extend into the cardiac chamber (Figure 2E; Table 2). The rake-like first row, lining the anterodorsal margin, protrudes anteriorly, and comprises type 1 spines of varying length. These spines are short at the medial base of the lateralia, but increase in length on the curvature of the anterior laterale. Those close to the side of the wall are

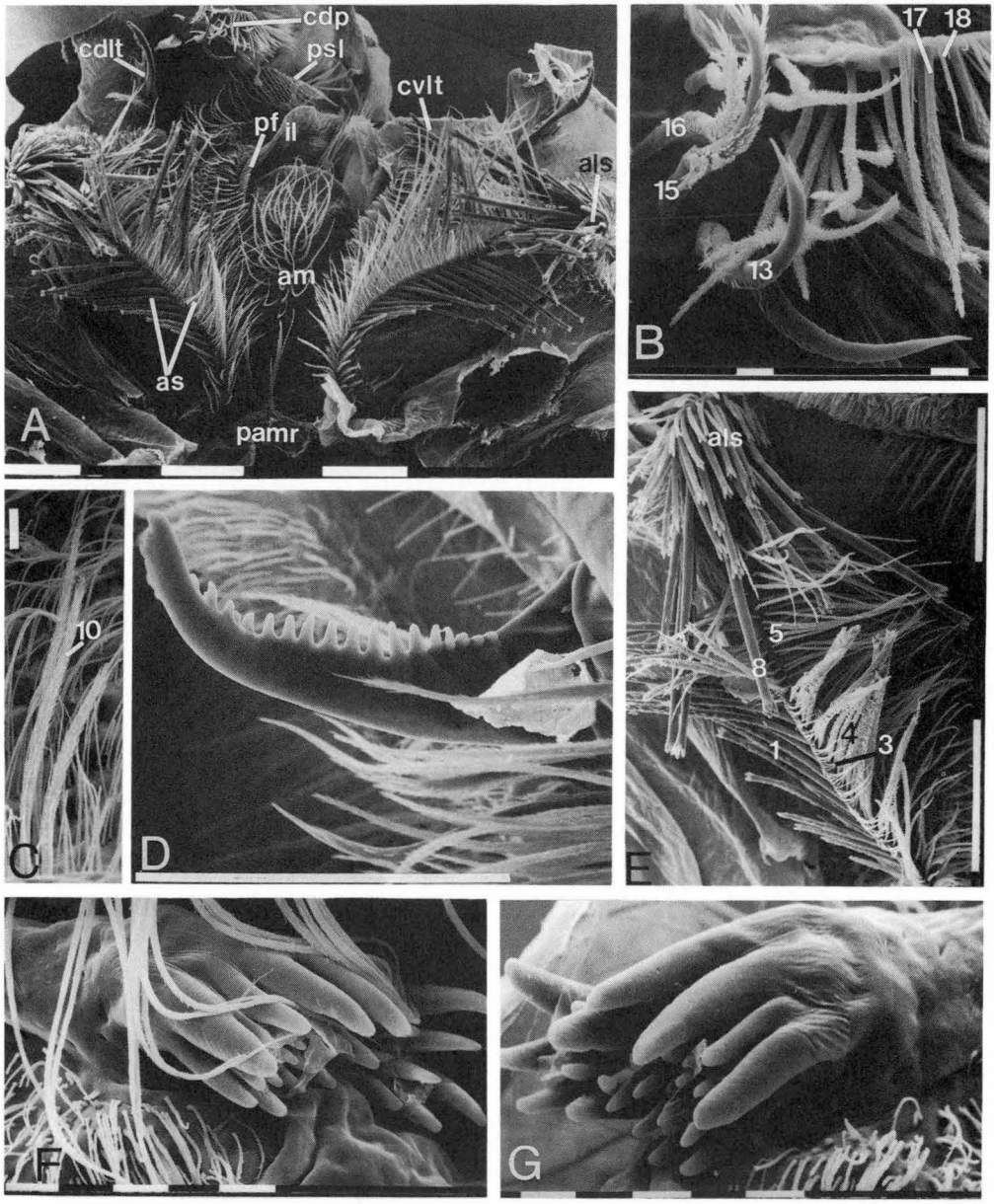

Figure 2. SEM micrographs of *Paramesopodopsis rufa* foregut. (A) Anterodorsal view with dorsal wall removed showing als, am, as, cdlt, cdp, cvlt, il, pamr, pf, psl. (B) Types 13, 15, 16, 17, 18 spines of cdp (right half). (C) Type 10 spine. (D) Right cardiac dorsolateral tooth. (E) Dorsal view of right anterior laterale showing rows of types 1, 3, 4, 5 spines, and type 8 anterior laterale spine. (F) Right cardiac ventrolateral tooth. (G) Left cardiac ventrolateral tooth. Abbreviations as in Figure 1. For description of spine type see Table 2. Scale bars: A,D&E, 0·1 mm; B,C,F&G, 10 μm.

Table 1. *Size and foregut morphometrics (mean ±SD) for the three species of mysids.*

	Paramesopodopsis rufa	*Anisomysis mixta australis*	*Tenagomysis tasmaniae*
Size (mm)	9.45 ±0.42	6.08 ±0.15	7 85 ±0.38
Length-specific gut capacity (mm^2)	0.044 ±0.005***	0 006±0.001***	0.020 ±0.003***
FGI (%)	89 6 ±5.2^{ns}	95.0 ±4 1^{ns}	86.8 ±8.0^{ns}

N=15 ***, highly significant difference ($P<0.001$, Tukey's HSD test) when compared to values from other species; ^{ns}, no significant difference ($P>0.05$, Kruskal-Wallis test) when compared to values from other species.

shorter. The second row is made up of type 3 spines which are curved posteriorly. Type 4 spines comprise the rake-like third row. The fourth row consists of type 5 spines which line the posterodorsal margins of the anterior lateralia. These spines are also found on the remainder of the surface of the laterale. The anterior lateral spines appear as a cluster of type 8 spines arising from the point where the anterior laterale merge with the lateral wall of the stomach (Figure 2A,E; Table 2). These spines vary in length; shorter spines surround the outer part of the cluster, while those on the central portion are longer and inter-digitate with the rows of spines on the laterodorsal margin of the anterior lateralia. The surface of the remainder of the laterale bears types 3 and 5 spines (Table 2). The posterior lateral spines are type 10 (Figure 2C; Table 2). On the ventromedial margin of the lateralia, several rows of type 6 spines project medially (Table 2).

The dorsal surface of the anteromedianum bears 25-30 long stout spines which are curved posteriorly (Figure 2A). This patch of setae form a V-shaped pattern. The cardiac dorsolateral tooth (CDLT) projects anteromedially from a broad base (Figure 2A,D). The ventral margin of the tooth is rounded and free from any dentition, while the dorsal portion is flattened and bears 11 short denticles arranged like comb blades. Distally, the rounded ventral portion becomes cylindrical, and short, stout spinules are found on its dorsal surface. Just posterior to the CDLT, and before the entrance to the pyloric dorsal food channel, there is a patch of long, posteriorly-directed spines. Below these spines protrudes the cardiac ventrolateral tooth (CVLT) (Figure 2A,F&G). Each CVLT comprises a cluster of 20-22 smooth, finger-like spines.

The cardiac dorsal piece (CDP), which is basically a group of spines hanging from a ridge in the roof of the cardio-pyloric junction, lies between the pair of cardiac dorsolateral teeth (Figure 2A). The CDP comprises types 13, 15, 16, 17, and 18 spines (Figure 2B).

Anisomysis mixta australis

Although *A. mixta australis* showed the smallest gut volume, its FGI is similar to those in the other two species (Table 1). Like the other two species, the anterior surface of the laterale is bare, but four type 2 spines project on its anterodorsal margin (Figure 3A; Table 2). A posterior second row of type 3 spines is also present (Figure 3B,C; Table 2). Next to the second row, on the posterior surface of the margin, is the third row of type 4 spines (Figure 3B,C;Table 2). The remainder of the surface of the laterale, except its ventral and dorsolateral margins, is sparsely covered only with type 3 spines (Figure

Table 2. *Macrospines on the lateralia and the cardiac dorsal piece of the foregut of the three mysid species. Number in parenthesis represents type.*

Location	*Paramesopodopsis rufa*	*Anisomysis mixta australis*	*Tenagomysis tasmaniae*
Anterodorsal margin of the anterior laterale	round-based, stout, stiff, distal half of shaft with sharp broad-based spinules, 3 pronged-tip (1)	round-based, less stout than (1), stiff, entire shaft and tip with slim-based spinules (2)	(1)
	round-based, curved, thin, short, forms second row, with few minute spinules (3)	(3)	(3)
Dorsal margin of the anterior laterale	flat-based, curved, with thin spinules on shaft (4)	(4)	(4)
Posterodorsal margin of the anterior laterale	round-based, thin, long with fine spinules on shaft (5)		(4)
Ventromedial margin of the laterale	round-based, distal half of shaft with spinules (6)	(6)	
Remainder of the anterior laterale	(3), (5)	only (3)	flat-based, stout, curved, with minute thin spinules (7), and (3), (5)
Anterior lateral margin of the laterale	stout,4-7 pronged-tip with 1 central prong and the rest peripheral, spines form a cluster (8)	stout, 7-10 pronged-tip, prongs arranged as in (8), bifid tip (9)	(8)
Posterior lateral margin of the laterale	flat-based, long, stiff, with slim-based spinules on shaft (10)	round-based stout, short, pointed tip, with few sharp, slim-based spinules on shaft (11)	flat-based, robust, tooth-like pointed tip, with sharp, broad-based spinules on shaft (12)
Cardiac dorsal piece	round-based, stout, forms J-shaped curve, with a row of spatulate spinules following curvature of shaft (13)	as in (13) but less stout, with >1 rows of spinules on shaft (14)	(13), (15), (16)
	as in (13), but with >1 rows of spinules on shaft (15)		
	round-based, less stout, with dense fine spinules on distal half of shaft and tip (16)		
	round based, thinner than (16), sparse spinulation on three-quarters of shaft (17)	(17)	(17)
	round-based, thin, and short, with few alternate spinules on shaft (18)		

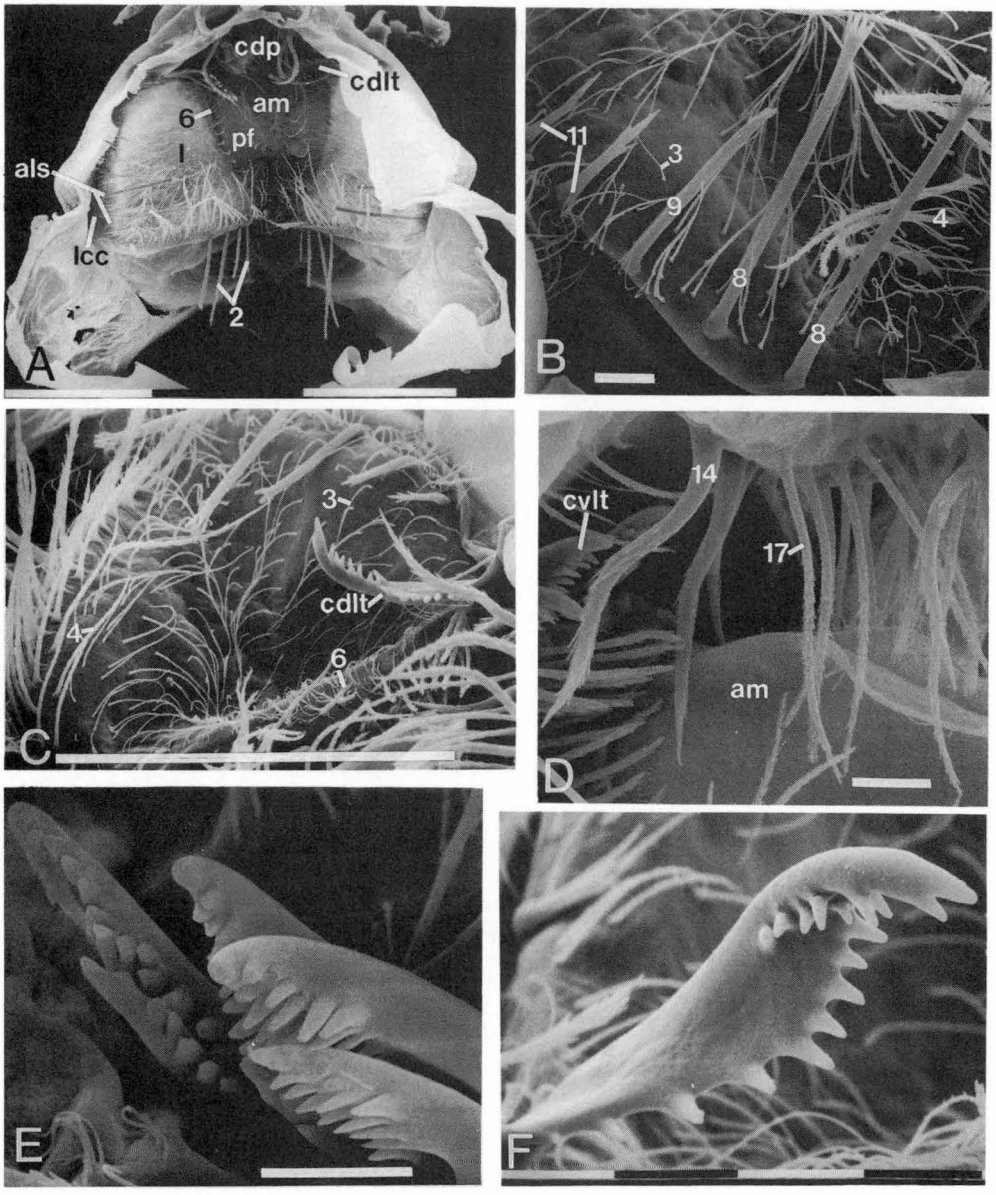

Figure 3. SEM micrographs of *Anisomysis mixta australis* foregut. (A) Dorsal view with dorsal wall removed showing als, am, cdlt, cdp, l, lcc, pf, and types 2 and 6 spines. (B) Types 3, 4, 8, 9, and 11 spines of laterale. (C) Side view of laterale showing cdlt and types 3, 4, 6 spines. (D) Types 14 and 17 spines of cdp (right half), and portions of am and right cvlt. (E) Left cardiac ventrolateral tooth. (F) Left cardiac dorsolateral tooth. Abbreviations as in Figure 1. For description of spine type see Table 2. Scale bars: A&C, 0·1 mm; B,D,E&F, 10 μm.

3C). The lateral margins of the laterale bear two pairs of type 8 spines as their anterior lateral spines (ALS). These spines are longer than the two pairs of type 11 and a pair of type 9 posterior lateral spines (PLS) that are also present (Figure 3B; Table 2). Although these spines resemble those found on the ALS of *Paramesopodopsis rufa* and *Tenagomysis*

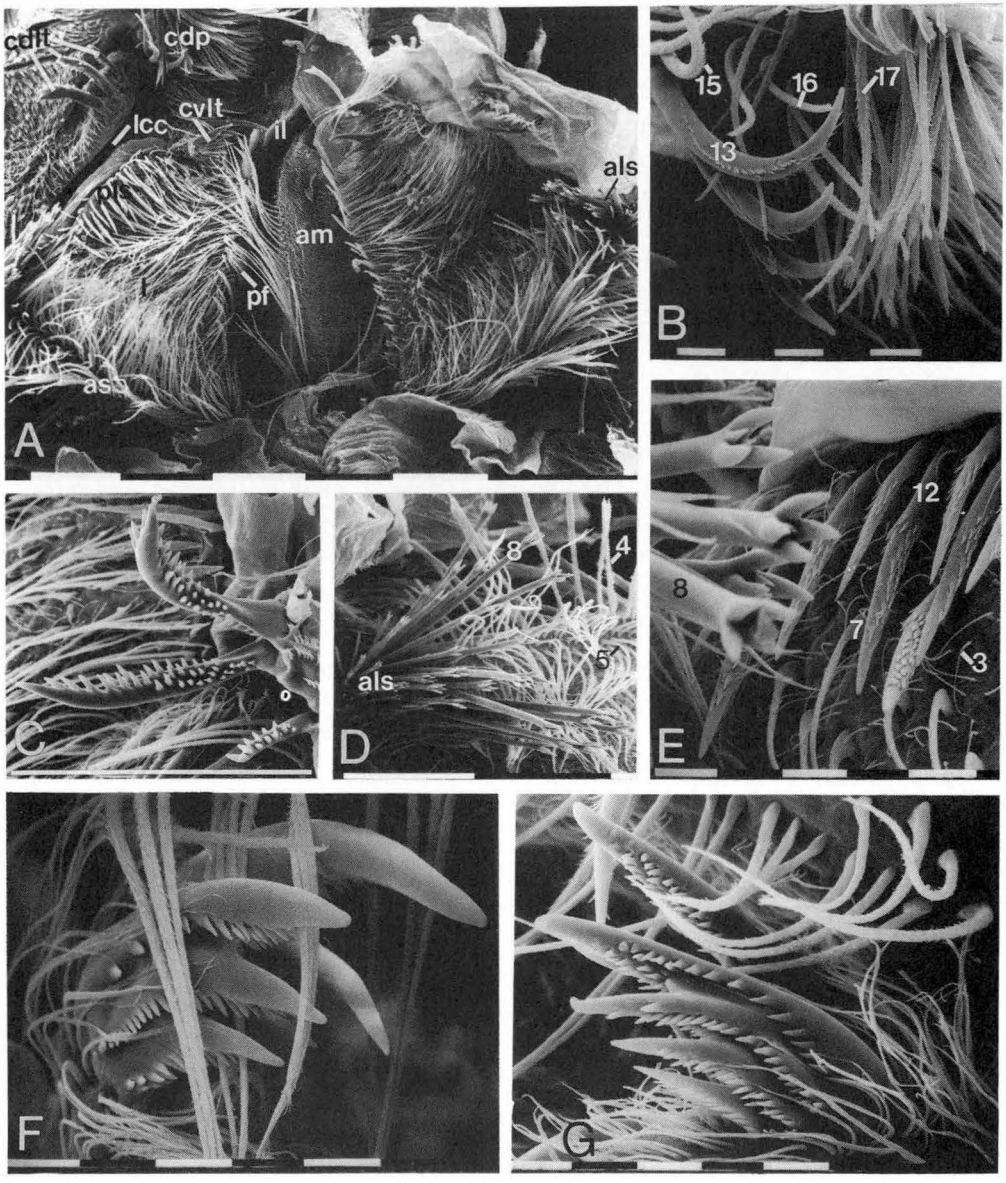

Figure 4. SEM micrographs of *Tenagomysis tasmaniae* foregut. (A) Anterodorsal view with dorsal wall removed showing als, am, as, cdlt, cdp, cvlt, il, l, lcc, pf, pls. (B) Types 13, 15, 16, 17 spines of cdp (right half). (C) Right cardiac dorsolateral teeth. (D) Types 4 and 8 spines of laterale. (E) Types 3, 7, 12 spines of laterale, and type 8 spine pronged tips. (F) Right cardiac ventrolateral tooth. (G) Left cardiac ventrolateral tooth. Abbreviations as in Figure 1. For description of spine type see Table 2. Scale bars: A,C&D, 0·1 mm; B,E,F&G, 10 μm.

tasmaniae, they are isolated and do not form a cluster. The ventromedial margin of the lateralia possesses a widely-spaced row of type 6 spines (Figure 3A,C; Table 2).

Sixteen long stout spines which are curved posteriorly adorn the dorsal median region of the anteromedianum (Figure 3A). Like in *P. rufa*, these spines form a V-

shaped pattern of distribution. The stout, curved cardiac dorsolateral tooth (CDLT) projects anteromedially above the posterior region of the anteromedianum (Figure 3A,C&F). Both CDLT extending from the dorsal wall of the stomach are arranged symmetrically. Each tooth is fringed with small, blunt teeth (Figure 3F). Between 19 and 21 small denticles are present, but only on the margins and distal portion of the tooth. The cardiac ventrolateral tooth (CVLT) is formed by a cluster of barbed spines (Figure 3D,E). Five stout spines form the cluster, and each of the three additional dorsal spines is endowed with broad-based blunt denticles on the ventral surface of the shaft.

The cardiac dorsal piece (CDP) consists only of type 14 spines on its side and type 17 spines in the middle (Figure 3D; Table 2).

Tenagomysis tasmaniae

The foregut volume of *T. tasmaniae* is almost half that measured in *P. rufa*, while its FGI is similar to that of the other two species (Table 1). As in *P. rufa*, the anterodorsal and dorsal margin of the anterior lateralia possess four rows of similar types of spines (Table 2). The posterodorsal margin bears type 4 spines (Figure 4D). The remainder of the surface of the laterale comprises types 3, 7 (Figure 4E; Table 2) and 5 (Figure 4D) spines. Although the tips of the anterior lateral spines (ALS) appear sharper in *T. tasmaniae*, the structure and arrangement of the ALS are very similar to those in *P. rufa* (Figure 4A,D). The posterior lateral spines consist of a pointed, robust, sharply-barbed type 12 spine (Figure 4E; Table 2). In *T. tasmaniae*, the ventromedial margin of the lateralia bears no type 6 spines which are present in the other two species.

The anteromedianum, distinct in *T. tasmaniae*, has a pointed apex and a narrower base (Figure 4A). In contrast, in the other two species the anteromedianum is almost dome-shaped and has a broad base. The anterior three quarters of the anteromedianum's pinnacle bears a row of 17 long, bristled spines which curve posteriorly. Three symmetrical pairs of cardiac dorsolateral teeth (CDLT) are present (Figure 4A,C). The two anterior teeth are larger than the more posterior tooth. The teeth are prominent processes dorsal to the lateral circulation channel. Rows of very sharp denticles arm the dorsal surface of each tooth. The cardiac ventrolateral teeth (CVLT) of *T. tasmaniae* appear as a cluster of seven saw-like spines (Figure 4A,F&G).

The cardiac dorsal piece (CDP) in *T. tasmaniae* closely resembles that of *P. rufa* (Figure 4A,B). The structure is also composed of types 13, 15, 16, and 17 spines (Figure 4B).

DISCUSSION

It is widely recognized that the gross structure of mysid foreguts is similar to the eucaridan (Euphausiacea and Decapoda) proventriculus or gastric mill (Gelderd, 1909; Haffer 1965; Mauchline, 1980; Fretter & Graham, 1976; Storch, 1989; Ullrich *et al.*, 1991), and to the foregut of other peracarids (*e.g.* Storch, 1987, isopod; Icely & Nott, 1984, amphipod). These similar features are shared by the three mysid species examined here, but apparent differences are also observed. These differences in structure and probable function, and the possible evolutionary feeding lines are summarized in Table 3.

Table 3. *Foregut features and their probable function (in parentheses), and possible evolutionary feeding lines of the three mysid species.*

Spination pattern on lateralia	*Paramesopodopsis rufa*	*Anisomysis mixta australis*	*Tenagomysis tasmaniae*
Anterior margin	>1 rows of both stout (prong tipped) and thin spines (raking large clumps of food from anterior to posterior chamber)	single row of thin spines (pushing finer and softer food particles)	as in *P. rufa*
Remainder of the surface	dense and different types (pushing large bulky food)	only type 3 spines (pushing finer and softer food)	denser and more diverse than in *P. rufa;* spine types with sharp cusps (pushing and shearing large bulky food)
Anterior lateral spines (ALS)	clustered with pronged tips (pushing, cutting, shearing large food particles)	spines isolated and few (pushing and shearing smaller food particles)	clustered with pronged tips (as in *P. rufa* but possibly more powerful
Cardiac dorsal piece (CDP)	more spines of the stout curved type (type 16) (pushing larger food mass into posterior foregut)	few spines without the stout curved type (pushing smaller food mass into posterior foregut)	as in *P. rufa*
Cardiac dorsolateral teeth (CDLT)	as in *A. mixta australis*	single with few blunt cusps (transporting clumps of food; limited cutting function)	three with many sharp cusps (cutting and transporting clumps of food)
Cardiac ventrolateral teeth (CVLT)	clustered with no dentition (squeezing and grinding)	clustered with blunt dentition (squeezing, grinding and some degree of cutting)	clustered with sharp dentition (squeezing, piercing, grinding and cutting)
Possible evolutionary feeding line (after Kunze & Anderson, 1979)	Type IIa: predominantly macrophagous (mainly predatory, necrophagous, detritivorous)	Type I: predominantly microphagous (mainly feeds on fine particulate matter)	Type IIb: predominantly macrophagous (mainly feeds on tough plant detritus)

Storch (1989) noted that cuticular projections on the lateralia may act to push the food posteriorly. The series of rows of spines cannot be interpreted as a passive sieve (Nath & Pillai, 1973) because the action of the intrinsic and extrinsic muscles associated with the lateralia would certainly impart active movements to these structures. Activity of these structures is likely to keep coarser food particles in the dorsal region of the cardiac stomach, and the finer particles in the ventral region (Storch, 1989). As well as aiding the rows of spines on the margin of the anterior lateralia in translocating large and bulky food from the anterior cardiac chamber, the anterior lateral spines (ALS) may also press the food mass against the primary filter for the initial straining. Furthermore, they dovetail to each other, and in the process of pressing, individual spines probably exert

a shearing action. In this manner, some food components may be ground to a pulpy consistency. Co-ordinated by extrinsic and intrinsic muscle contraction (Haffer, 1965), the ALS may also push the food towards the cardio-pyloric junction where food is further processed by the cusped cardiac dorsolateral teeth (CDLT) and ventrolateral teeth (CVLT). The cardiac dorsal piece (CDP) has been suggested as pushing food masses into the more posterior region of the foregut (Storch, 1989).

Fretter & Graham (1976) suggested that tooth-bearing ridges at the junction between the cardiac and pyloric chambers process the food, keep coarser food particles away from the ventral passages of the pyloric chamber, and regulate passage towards the midgut. The CDLT and CVLT are found in the region of the foregut where a prominent set of extrinsic muscles originates (Haffer, 1965). The action of these muscles moves these teeth, and depending on the integrity of these structures, therefore also the food-processing action. Ullrich *et al.* (1991) have noted that in *Euphausia superba,* the foregut regions, where the lateral teeth and cluster spines are associated (structures possibly homologous to the CDLT and CVLT in mysids), display activities that indicate a crushing and triturating function.

The differences in gut volume of the three species do indicate another possible adaptation to diet. The FGI developed by Suh & Nemoto (1988) seems to obscure the apparent function of the foregut, particularly the cardiac chamber, because it does not take into account its three-dimensional nature. *Paramesopodopsis rufa,* the primarily carnivorous species, has the largest length-specific gut volume, while the primarily fine, particulate feeder *Anisomysis mixta australis* (due to size) showed the smallest volume; and *Tenagomysis tasmaniae,* the algal detritus feeder, showed gut volumes half those of *P. rufa.* Studies on other peracarids have shown that the foreguts of mainly carnivorous-necrophagous species differ from those of mainly herbivorous or detritivorous species by having large volumes which have been suggested to be an adaptation to storing large and soft food materials typical of animal prey only present for short periods (*e.g.* Keith, 1974; Jones, 1968; Sheader & Evans, 1975; Icely & Nott, 1984; Hassall, 1977). Similar observations have been noted by Nemoto (1977) in the bathypelagic carnivorous thysanopod euphausiids. The elaborate distribution of spines in *T. tasmaniae* (relatively detritivorous) and a relatively small gut capacity may be associated with the rapid removal of macrophyte detritus (less nutritious) from the gut (Calow 1981; Zagursky & Feller, 1985). Aside from food particle size, the availability, diversity, and nutritional value are also reflected in gut structure (Icely & Nott, 1984).

In euphausiids, internal gut armature may be more taxonomically than diet related (Suh & Nemoto, 1988; Suh, 1990). The digestive system of other decapods depends primarily on the phylogenetic history of the species, but can be modified partially by other factors such as diet (Kunze, 1981; Felgenhauer & Abele, 1989; Icely & Nott, 1992). The three mysid species belong to the same Sub-Family (Mysinae) (Fenton, 1986), and although they belong to different Tribes (both *P. rufa* and *A. mixta australis* belong to the Tribe Mysini while *T. Tasmaniae* belongs to the Tribe Leptomysini) some foregut features are similar in both Tribes and some features are not shared (see Table 3). Phylogenetic history, in the present context, is weak in explaining the differences in foregut armature. To our knowledge, this is the first comparative study on the fine

foregut structure of mysids with known diet, and the features of the internal gut armature shown by the three species are in keeping with the theory that the feeding apparatus is adapted to cope with the various types of food resource utilized by the animal (Fryer, 1977; Icely & Nott, 1992).

Species with similar trophic ecologies may coexist by partitioning of feeding niches as indicated by differences in feeding structures (Schoener, 1974). Webb & Wooldridge (1989) noted that the differences in gut armatures allow two co-occurring mysid species to utilize overlapping portions of the food resource. Icely & Nott (1992) suggested that subtle modifications in the gastric mill allowed four closely-related species of fiddler crabs to cohabit by specializing in different niches. Aside from habitat and food resource partitioning (Fenton, 1986), the morphological evidence presented here may also help to explain the co-occurrence of these three mysid species.

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